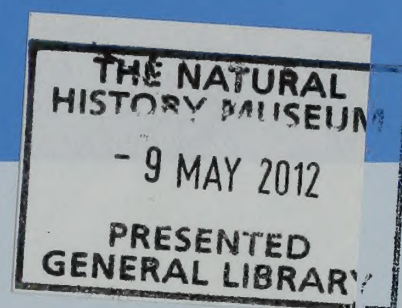


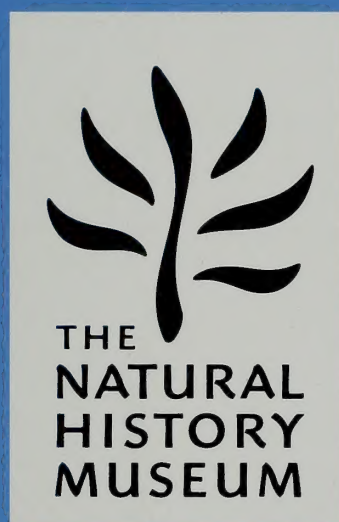
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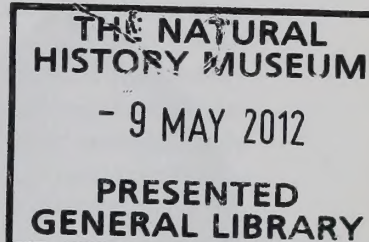
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Terebratula californiana Küster, 1844, and reappraisal of west coast north American brachiopod species referred to the genus *Laqueus* Dall, 1870



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SYNOPSIS. Dall defined the Recent brachiopod genus *Laqueus* primarily on adult loop characteristics of the dorsal valve interior of a specimen in the US National Museum collection. However, he designated as the 'type species' *Terebratula californica* Koch in Küster, a taxon erected by Küster and based only on a single specimen consisting of conjoined valves exhibiting features of only the shell exterior. Küster's holotype is apparently lost; however, a restudy of available early figured material allegedly from California and attributed to *Terebratula californica* (more correctly, *T. californiana* Küster) by Dall, Sowerby and Davidson indicates a very high probability that Küster's holotype was misidentified by Dall. Further, Küster's holotype almost certainly did not originate from Californian waters, but more likely was collected from off Coquimbo, Chile, and is referable to, or closely allied to, *Magellania venosa* (Solander, 1789) which has a known geographic range extending from Coquimbo, Chile, to the Straits of Magellan and the Falkland Islands. Under Article 70.3 of the Rules of Nomenclature, we designate *Laqueus erythraeus* Dall, 1920, as the type species of the genus *Laqueus* Dall. Specimens previously referred to *Laqueus californianus* (or *californicus*) from Californian waters are now referred to *Laqueus erythraeus* Dall, 1920. Specimens referred by other authors (listed in the Appendix) to *Laqueus californianus* (or *californicus*) occurring along the coasts of Washington, British Columbia and Alaska are now referred to *Laqueus vancouveriensis* Davidson, 1887.

INTRODUCTION

During the course of taxonomic reappraisals of diagnoses of brachiopod genera for the Treatise on Invertebrate Paleontology, Part H (currently under revision), an extensive literature search and investigation of available type and figured material of the genus *Laqueus* Dall, 1870, was undertaken. The investigation uncovered nomenclatural irregularities, including misinterpretation of the type species on which the genus *Laqueus* was founded, as well as frequent inconsistencies in the application of specific names to material collected along the Pacific coast of North America from California to Alaska (see Appendix). Given the longstanding importance of the genus in studies of Recent brachiopods we decided to undertake a critical review of the scientific literature that has dealt, over the past 130 years, with *Laqueus* species that occur in North American Pacific waters, with a view both to identifying and correcting past taxonomic irregularities and, equally importantly, promoting future stability of nomenclature of *Laqueus* species. We attribute much of the past confusion to the use by Dall (1870) of a specimen other than the holotype of the type species as the basis of his original generic diagnosis, and the failure of previous authors to establish the true identity and provenance of Dall's originally designated type species, *Terebratula californiana* Küster, 1844.

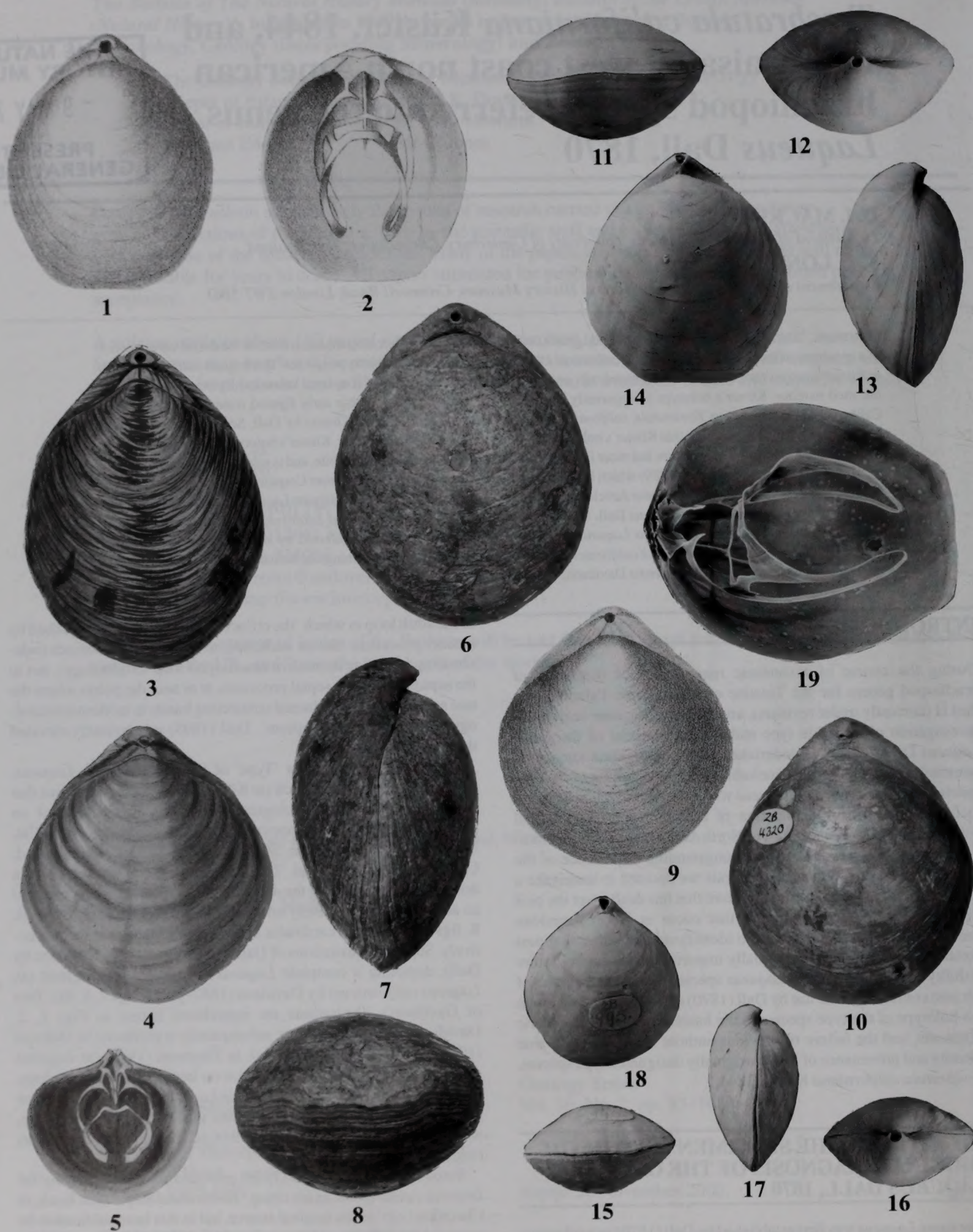
IDENTITY OF THE SPECIMEN USED IN THE ORIGINAL DIAGNOSIS OF THE GENUS *LAQUEUS* DALL, 1870

The name *Laqueus* was first established by Dall (1870) as a subgenus of *Terebratella* for brachiopods characterized by a distinctive form

of the adult loop in which 'the reflected part of the loop is attached by slender processes, one on each side, to the haemal processes (=descending branches in modern brachiopod loop terminology), not to the septum nor to the septal processes, at or near the points where the two septal processes (=lateral connecting bands in modern terminology) branch off to the septum'. Dall (1895) subsequently elevated the taxon to genus level.

Dall (1870) specified as 'Type' of his new subgenus *Laqueus*, *Terebratula californica* Koch (in Küster, 1844), but it is evident that his accompanying morphological description was based not on Küster's original figured specimen, but on a USNM specimen (Cat. No. 19395) collected from '80 fathoms, off Santa Catalina Island, California'. Dall (1870: pl. 7, fig. f) provided one illustration of a dorsal interior exhibiting the definitive adult *Laqueus* loop form, and an additional two relatively uninformative sketches (Dall, 1870: pl. 8, figs 9, 10) of the cardinalia and posterior shell exterior respectively. Superior illustrations of Dall's specimen (lent to Davidson by Dall), depicting a complete *Laqueus* loop, were also figured (as *Laqueus californicus*) by Davidson (1887: pl. 18, figs 7, 8, 8a). Two of Davidson's illustrations are reproduced herein as Figs 1, 2. Davidson's illustrations were subsequently reproduced in Oldroyd (1924) (as *Laqueus californicus*), in Thomson (1927) (as *Laqueus californicus*), and also in the Treatise on Invertebrate Paleontology, Part H, Brachiopoda (Hatai, 1965) (as *Laqueus californianus*). New photographic illustrations of the entire specimen, now minus loop, were figured by Hertlein & Grant (1944: pl. 21, figs 1–7) (as *Laqueus californianus*).

Some 50 years later, Dall (1920) provided another synonymy for *Laqueus californicus*, again citing '*Terebratula californica* Koch, in Chemnitz (*sic*)' as his original source, but in this later publication he removed the sole figured specimen of his 1870 publication (USNM Cat. No. 19395 – the specimen widely figured in later publications



on account of its distinctive loop) and designated that specimen the holotype of a new species *Laqueus erythraeus* Dall.

PROBABLE IDENTITY AND PROVENANCE OF THE HOLOTYPE OF *TEREBRATULA CALIFORNIANA* KÜSTER, 1844, ORIGINALLY DESIGNATED TYPE SPECIES OF THE GENUS *LAQUEUS* DALL

KÜSTER'S ORIGINAL TYPE SPECIMEN. Dall (1870) specified as 'Type' of his new subgenus *Laqueus*, '*Terebratula californica* Koch, Küster' 1844 (plate) 1848 (text). [Note: Dall's species name '*californica*' is a misspelling of Küster's original '*californiana*'; it is likely that Dall's misspelling (and the subsequent misspelling by various later authors) derives from an earlier misspelling by Sowerby (1846), followed by Carpenter (1864). Dall (and Carpenter) also followed Küster in incorrectly attributing the authorship of *T. californica* to Koch]. Küster inserted '*Terebratula californiana* Koch in litt.' immediately after his concise Latin diagnosis, but there is no record of Koch having ever formally published a description of the specimen described by Küster. Küster (1844: pl. 2b, figs 21–23) figured three views (dorsal, lateral and ventral) of the exterior of a single, large specimen with tightly conjoined valves but gave no interior views depicting the loop, or any other diagnostic internal characters. We refigure Küster's original illustration of the dorsal view as Fig. 3. Küster stated the locality as 'California' but gave no further details. The original description of *T. californiana* is somewhat unusual in that the species was named and illustrated by Küster in a part of his monumental revision of the 'Martini-Chemnitz Conchylien Cabinet' (second edition) that was published in 1844, whereas the description was not published until 1848.

Küster's holotype of *Terebratula californiana* could not be located by us and is presumed lost. However, his illustrations compare well with several specimens that were available to us in the brachiopod collections of The Natural History Museum, London, also attributed to the same species by near contemporaries of Küster, including Sowerby and Davidson, and placed in synonymy with *T. californiana* by Dall (1870 and 1920).

SOWERBY'S (1846) FIGURED SPECIMENS OF *TEREBRATULA CALIFORNICA*. In his synonymy of the type species of his new subgenus *Laqueus*, Dall (1870) listed a second reference to *Terebratula californica* Koch, that of Sowerby (1846) (the perpetrator of the original misspelling of *californiana* as *californica*), whose illustrations (Sowerby, 1846: pl. 70, figs 50–52) consisted of two exterior views and one dorsal interior with complete loop. Two of Sowerby's illustrations are refigured herein as Figs 4, 5. It must be stressed that the (teloform) loop structure depicted by Sowerby (op. cit.: pl. 70, fig. 52 and refigured herein as Fig. 5) for his *Terebratula californica* is quite dissimilar to that (bilateral) figured by Dall (1870: pl. 7, fig. f and refigured herein as Fig. 2) for allegedly the

same species (see Richardson, 1975, for explanations of brachiopod loop terminology, viz. teloform and bilateral). Sowerby's figured teloform loop is, however, comparable to that occurring in *Magellania venosa* (Solander, 1789). Indeed it is apparent that Dall (1920) subsequently recognized the discrepancy in the form of the Sowerby figured loop for, in his 1920 synonymy of *Laqueus californicus*, he again cited Sowerby (1847 (*sic*)), but this time included only Sowerby's two exterior views (plate 70, figs 50, 51) and specifically excluded Sowerby's interior with the teloform loop (plate 70, fig. 52) which he referred to *Magellania*.

DAVIDSON'S FIGURED SPECIMENS OF *LAQUEUS CALIFORNICUS*. Davidson (1887) was the first to take account of possible geographic variation in *L. californicus* by referring specimens collected from higher latitudes to a separate 'variety', *L. californicus* var. *vancouveriensis*, whilst retaining the binomen *L. californicus* for specimens hitherto known from Californian waters. It is our opinion that Davidson, in fact, presented illustrations of three distinct species, namely: (1) the Dall specimen (USNM 19395) from Santa Catalina Island, illustrating the *Laqueus* loop (Davidson, 1887: pl. 18, figs 7, 8, 8a); (2) two large specimens (including ZB 4417) attributable to Küster's species (Davidson, 1887: pl. 18, figs 6a–c, 9); (3) the specimens from higher latitudes attributed by Davidson to *L. californicus* var. *vancouveriensis* (Davidson, 1887: pl. 18, figs 10–13).

1. The Dall specimen (USNM 13395) (Figs 1, 2). This is the specimen which Dall (1920) subsequently designated as the holotype of *L. erythraeus*. We do not consider the specimen USNM 13395 to be conspecific with the Küster holotype. As the loop of Dall's diagnostic specimen is no longer preserved, Davidson's illustration of the loop (widely reproduced in later publications; Fig. 2) provides the best record of its appearance.
2. The specimens attributable to Küster's species. Davidson (1887: pl. 18, figs 6, 6a, 6b) figured three views of a large specimen (ZB 4417) with conjoined valves that bear very close resemblance in size, shape and appearance, to Küster's holotype of *Terebratula californiana*. Specimen ZB 4417 is well documented in The Natural History Museum's brachiopod collection as the specimen illustrated in Davidson (reproduced herein as Figs 6–8). There is no explicit documentation in The Natural History Museum's collections of the second specimen (Davidson, 1887: pl. 18, fig. 9; reproduced herein as Fig. 9) attributed to *Laqueus californicus* which, according to Davidson, is a reproduction of Küster's illustration (1844: pl. 2d, figs 1–3) of *Terebratula kochii* (Davidson's figure caption, p. 178, mistakenly quotes the Küster figure reference as 'tab. 2a, fig. 9' for this specimen).

Davidson's specimen (ZB 4417) with conjoined valves, still bearing original labelling, was examined by us and although the strong articulation of the valves precluded their total separation, it was possible to open the valves sufficiently to confirm that, despite the absence of a loop due to breakage, the internal morphology was unlike that attributable to any species of *Laqueus*.

Figs 1–19 Illustrations of specimens that have in the past been assigned to the genus *Laqueus* Dall. **1, 2**, Davidson's illustrations (Davidson 1887: pl. 18, figs 7, 8) of the USNM specimen 19395 assigned by him to *Laqueus californicus*, originally figured by Dall (1870), showing the distinctive *Laqueus* loop, × 1. **3**, Küster's original illustration of the holotype of *Terebratula californiana* (Küster 1844: pl. 2b, fig. 21), × 1. **4, 5**, Sowerby's illustrations (Sowerby 1846: pl. 70, figs 50, 52) of *Terebratula californica*, × 1. **6–8**, dorsal, lateral and anterior views of NHM specimen ZB 4417 assigned by Davidson (1887: pl. 18, figs 6, 6a, 6b) to *Laqueus californicus*, × 1. **9**, Davidson's illustration (Davidson 1887: pl. 18, fig. 9) of Küster's *Terebratula kochii*, assigned by Davidson to *L. californicus*, × 1. **10**, dorsal view of NHM specimen ZB 4320 of *Terebratula (Waldheimia) globosa* figured by Reeve (1860: pl. 2, species 3, fig. c), × 1. **11–14**, anterior, posterior, lateral and dorsal views of NHM specimen of *Laqueus erythraeus* Dall, ZB1001, × 1. **15–18**, anterior, posterior, lateral and dorsal views of NHM specimen of *Laqueus vancouveriensis* Davidson, ZB995, × 1. **19**, dorsal oblique view of dorsal interior of *Laqueus erythraeus* showing the loop, ZB4505, × 1.5.

We consider the internal morphology of this Davidson specimen (ZB 4417) suggests close affinity with *Magellania venosa* (Solander, 1789) which is unknown from Californian waters, and has a known range from Coquimbo, Chile, to the Straits of Magellan and the Falkland Islands. We also consider that the second specimen referred by Davidson to *L. californicus* (Davidson, 1887: pl. 18, fig. 9) should be referred to the genus *Magellania* (aff. *M. venosa*). Indeed the Davidson specimen (ZB 4417) bears strong resemblance both internally and externally to the '*Terebratula* (*Waldheimia*) *globosa*' figured by Reeve (1860: pl. 2, species 3, fig. c), and refigured by us as Fig. 9, which was synonymised by Davidson (1887: 112) with *Laqueus californicus*. The loop of Reeve's specimen (ZB 4320), though only partially intact, is unmistakably teloform (as in *M. venosa* but not *Laqueus*) and is almost certainly conspecific with the Davidson specimen (ZB 4417). Furthermore, Reeve quotes two localities viz. 'California, Coquimbo'. We are strongly of the opinion that the 'California' location attributed to Davidson's, Reeves', Sowerby's and Küster's specimens of *L. californicus* is erroneous and that Coquimbo (Chile) is a more likely source. The strong similarity of Davidson's, Reeves', and Sowerby's specimens of *L. californicus* (and the inferred similarity of the Küster holotype) to *Magellania venosa* is apparent but further investigation of the material is required, especially with regard to provenance.

3. The Vancouver Island specimens. According to Davidson (1887), Dall (personal communication, 1884) referred brachiopod assemblages from the vicinity of Vancouver Island, British Columbia, Canada, to *L. californicus*. Davidson considered the morphology of the Vancouver Island assemblages to be sufficiently different (smaller size, comparatively larger pedicle foramen) from his (undifferentiated) Californian assemblages to merit recognition as a distinct variety, namely *L. californicus* var. *vancouveriensis* and he illustrated them as such (Davidson, 1887: pl. 18, figs 10–13b). Adult specimens of Davidson's *L. californicus* var. *vancouveriensis* possess a typical *Laqueus* (bilateral) loop and are not considered by us to be conspecific with the Küster holotype.

LAQUEUS JEFFREYSI DALL, 1895. In his initial study, Dall (1870) erected only two species of *Laqueus*, namely *L. californicus* from Californian waters, and *L. suffusus* from Japan. Following examination of extensive collections (listed in Dall 1920: 348–349) made by the U.S. Fish Commission steamer Albatross from the Aleutian Islands to California, Dall (1895: 725) referred specimens of the Davidson variety *vancouveriensis* to a new species *L. jeffreysi*, and it is clear from Dall's discussion that he was applying the name *jeffreysi* to what he referred to informally as 'the northern form', whilst retaining the species name *californicus* for 'the southern form' occurring off Santa Catalina Island.

There is, however, confusion over the validity of the name *jeffreysi* for that species, as *jeffreysii* (*sic*) had been used previously by Dall in three separate publications (firstly as *Frenula jeffreysii* (*sic*) (Dall, 1871a: 55); secondly as *Ismenia? jeffreysi* (Dall, 1871b: 65); thirdly as *Megerlia* (*Ismenia*) *jeffreysi* (Dall, 1873: 187)) for small brachiopods presented to him by J. Gwyn Jeffreys that had been recovered from northeast Atlantic waters. In a fourth publication, Dall (1877) united the abovementioned northeast Atlantic specimens with additional brachiopods from the northeast Pacific, collected by Dall from the Semidi Islands and Port Etches and by J. Richardson from Vancouver Island, Victoria, British Columbia, all under the name *Megerlia jeffreysi*. Having erected the genus *Laqueus* in 1870, prior to the publication of his reports on those specimens to which he applied the species name *jeffreysi*, it is evident that Dall, at that time

(1877), did not consider any of his Northeast Pacific specimens to be referable to *Laqueus*. In his 1895 publication, however, it is evident that Dall had changed his mind, now referring *all* his previous *jeffreysi* specimens to the genus *Laqueus*. Subsequently, having by that time realized that the Northeast Atlantic specimens to which he originally applied the species name *jeffreysi* were, in fact, juveniles of *Macandrevia cranium* (Müller), Dall (1920) abandoned the use of *jeffreysi* and reverted to employing Davidson's 'variety', *Laqueus californicus vancouveriensis* for the U.S. National Museum's approximately 185 specimens of his 'northern form', occurring from 'South East Alaska Peninsula' to the 'Washington coast'. As well as listing the many specimens attributable to *Laqueus californicus vancouveriensis*, Dall (1920) also listed some forty specimens under the heading '*L. californicus*, typical', mainly from Californian waters, but the list excluded his specimens of the large reddish-tinted form from off Santa Catalina Island, which include specimen USNM 19395, for which Dall (1920) established his new species *Laqueus erythraeus*.

LAQUEUS ERYTHRAEUS DALL, 1920. Dall (1920) did not provide an accompanying morphological description of his new species, but it is obvious that since his original description of *L. californicus* (Dall, 1870) was based on specimen USNM Cat. No. 19395 from Santa Catalina Island, his 1870 description now (in 1920) applied to *L. erythraeus*. Whilst not explicitly saying so, Dall appeared to separate *L. erythraeus* from *L. californicus* (*sic*) on the basis of size, shape, colour, and possibly also biogeographic extent. The etymology of the species name *erythraeus* (from the Greek *erythros*, red) is a clear reference to the strong reddish shell coloration so typical of Californian specimens of *Laqueus*. Although it is clear that the holotype of *Laqueus erythraeus* is USNM 19395, Dall (1920) also included in his synonymy two references by Carpenter (1864). However, page citations in Carpenter (1864) contain no new descriptions or illustrations but are merely taxonomic listings of earlier authors. Carpenter's citation on page 568 refers to specimens of '*Terebratula* (*Waldheimia*) *globosa* (Val), Lam.' figured in Reeve's 'Conchologia Iconica; Terebratulidae' (Reeve, 1860) which he (Carpenter) synonymises with '*T. californica* Koch'. Carpenter's citation on page 574 refers to an entry in an earlier publication (Trochel's 'Archives für Natur') which reads '1849. Vol. II, p. 99 *Terebratula Californica*, Linsley'. Also listed in Dall's synonymy (Dall, 1920), was an additional Carpenter (1864) reference – '*Waldheimia californica* CARPENTER, Supple. Rep. Brit. Assoc., p. 636, 1864' – but this entry is part of a table of localities with no illustration or description given. Dall's references to Carpenter's earlier citations are thus erroneous and further confuse rather than assist any understanding of the new species, *L. erythraeus*.

Specimen USNM 19395 was subsequently figured by Hertlein & Grant (1944) as '*Laqueus californianus* Koch. Type of *Laqueus erythraeus* Dall'. Hertlein & Grant (1944: pl. 21, figs 1–7) figured five exterior and two interior views of specimen USNM 19395: the dorsal interior (previously figured by Dall and Davidson) no longer has the loop preserved. Hertlein & Grant (1944) rejected Dall's taxonomic revision, synonymising *L. erythraeus* once again with *L. californianus* and adding the statement (p. 146), '*Laqueus erythraeus* Dall appears to be an individual variation and not entitled to taxonomic recognition'. Hertlein & Grant were clearly unaware of any discrepancy in the identity of the originally designated holotype of *L. californianus*, viz. *Terebratula californiana* Küster, 1848 and on the basis of the evidence presented herein regarding the longstanding lack of awareness of the misidentified Küster type, we resurrect the species *L. erythraeus* (holotype USNM 19395) as a valid species and, under Article 70.3 of the Rules of Nomenclature (ICZN, 1999),

we herein designate *Laqueus erythraeus* Dall, 1920, as the type species of the genus *Laqueus* Dall, 1870.

LAQUEUS VANCOUVERIENSIS DAVIDSON, 1887. Davidson's *Laqueus californicus* var. *vancouveriensis* (Dall's 'northern form') was elevated to full species rank by Hertlein & Grant (1944) who provided a comprehensive synonymy and extensive biogeographic and stratigraphic records of the species. It is obvious that Hertlein & Grant applied the species name *vancouveriensis* to all material collected along the North American Pacific coast north of California, and were doubtful of earlier records of the species from Californian waters. We agree with Hertlein & Grant's differentiation of *vancouveriensis* as a full species. We are aware that various authors from the mid-1960's to the present have applied the name *Laqueus californianus* (or *californicus*) to specimens collected from waters off British Columbia and Washington (see Appendix). In line with Hertlein & Grant (1944) we believe that those specimens are more correctly referable to *Laqueus vancouveriensis* and we advocate that all future collections from north of California (exhibiting typical *L. vancouveriensis* morphology as described by Hertlein & Grant) be identified as such.

CONCLUSIONS

1. Küster's original holotype of *Terebratula californiana* was misidentified by Dall (1870). The holotype of *T. californiana* and various other specimens referred by nineteenth century workers to the species show strong affinity with *Magellania venosa* and were probably collected from waters off Coquimbo, Chile, not California. Consequently, use of the species name *californianus* (or *californicus*), as previously applied to North American *Laqueus* assemblages, should be abandoned.
2. Under Article 70.3 of the ICZN (1999), we herein designate *Laqueus erythraeus* Dall, 1920, as the type species of the genus *Laqueus* Dall, 1870.
3. Specimens previously referred to *Laqueus californianus* (or *californicus*) from Californian waters should now be referred to *Laqueus erythraeus* Dall, 1920.
4. Specimens previously referred to *Laqueus californianus* (or *californicus*) occurring along the coasts of Washington, British Columbia and Alaska should now be referred to *Laqueus vancouveriensis* Davidson, 1887.

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APPENDIX

Representative list of citations of northeast Pacific *Laqueus* species names (variously spelled) and localities referred to in the literature since 1924.

Laqueus californicus

- | | |
|---------------------|---|
| Oldroyd 1924 | British Columbia to off Point Loma, California. |
| Thomson 1927 | British Columbia to California (Recent); California (Pliocene). |
| Fraser 1932 | Nanaimo Region, Vancouver Island, British Columbia. |
| Staisny 1933 | Santa Catalina, California. |
| Nomura & Hatai 1937 | Off San Pedro, California. |
| Hatai 1938 | British Columbia to California (Recent); California (Pliocene). |

- Lowenstam 1961
Semenov 1965
Sass & Monroe 1967
Reynolds & McCammon 1977
Collins *et al.* 1988
Emig 1992

Laqueus californianus

- Smith & Gordon 1948
Hertlein & Grant 1944
Hertlein & Grant 1960

Bernard 1972

- Strathmann 1973
Thayer 1975, 1986
LaBarbera 1977, 1981, 1986

- Tunncliffe & Wilson 1988
Alexander 1990
Cohen & Gawthrop 1997
Cohen *et al.* 1998

Laqueus californicus convexus

- Konzhukova 1957

Laqueus californicus vancouverensis

- Oldroyd 1924

Thomson 1927

Laqueus vancouverensis

- Hatai 1938

Hertlein & Grant 1944

Laqueus aff. vancouverensis

- Weaver 1942

Laqueus vancouveriensis

- Hertlein & Grant 1960
Thayer 1986

Laqueus vancouveriensis diegensis

- Hertlein & Grant 1960

Laqueus erythraeus

- Oldroyd 1924
Thomson 1927

Laqueus jeffreysi

- Woodring *et al.* 1946

- Santa Catalina, California.
Gulf of Alaska.
Santa Catalina, California.
San Juan Island, Washington.
Friday Harbour, Washington.
San Juan Island, Washington.

- Point Pinos, Monterey Bay, California.
California.

- British Columbia to Point Loma, California; S. California (Middle Pliocene).

- Queen Charlotte Island, British Columbia to California and also the Sea of Japan.

- San Juan Island, Washington.

- San Juan Island, Washington.

- San Juan Island, Washington; Iceberg Point, Washington.

- British Columbia.

- Puget Sound.

- Bamfield, British Columbia.

- Bamfield, British Columbia.

- Tatar Strait, northern Sea of Japan.

- Southeast Alaska. Kodiak Island, Juneau

- Harbour, Forrester Island; off British Columbia; Juan de Fuca Strait, Puget Sound, Washington coast.

- S.E. Alaska to Washington; California (Pliocene).

- S.E. Alaska Peninsula to Washington; California (Pliocene).

- British Columbia.

- Olympic Peninsula, Washington to Queen Charlotte Island, British Columbia (Upper Eocene).

- Aleutian Island to Puget Sound.
Iceberg Point, Washington.

- South California, Lower California, Mexico (Middle Pliocene).

- Catalina Island, California.

- Catalina Island, California.

- San Pedro, California (Pleistocene).

Late Campanian-Maastrichtian corals from the United Arab Emirates-Oman border region

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SYNOPSIS. - 43 species of 34 genera of scleractinian corals and 1 genus of octocoral from the Qahlah and Simsima Formations of the United Arab Emirates-Oman border region are described. The faunas are dominated by colonial forms including the taxa *Actinastrea*, *Columactinastraea*, *Stylophora*, *Monticulastraea*, *Neocoenia*, *Stephanaxophyllia*, *Columastrea*, *Paraplococoenia*, *Astrogyra*, *Placosmia*, *Diplocoenia*, *Calamophylliopsis*, *Agathelia*, *Diploctenium*, *Cladophyllia*, *Glenarea*, *Dendrophyllia*, *Barysmilia*, *Orbignygyra*, *Astraraea*, *Pseudofavia*, *Goniopora*, *Actinacis*, *Brachycoenia*, *Mesomorpha*, *Fungiastrea*, *Brachyphyllia*, *Aspidastraea*. The occurrence of solitary corals is strongly dominated by *Cunulites*, with a minor appearance of *Montlivaltia*, *Aulosmilia*, *Phragmosmilia*, *Diegosmilia* and *Trochocyathus*.

INTRODUCTION

During the period 1991–1995 members of the Palaeontology Department of The Natural History Museum collected and described Upper Cretaceous macrofossils during their investigations of the Qahlah and Simsima Formations in the Oman Mountains of the United Arab Emirates-Oman border area. Previous results have been published on the lithofacies of the Qahlah and Simsima Formations (Smith *et al.*, 1995a), echinoids (Smith, 1995), ammonites (Kennedy, 1995), nautiloids and inoceramids (Morris, 1995), bryozoans (Taylor, 1995), brachiopods (Owen, 1995), and rudists (Morris & Skelton, 1995). In addition, studies on the palaeoenvironment dealing with echinoid-mollusc-coral assemblages provided the first information about the coral associations (Smith *et al.*, 1995b).

This paper adds to our knowledge of these Upper Cretaceous

faunas by providing a detailed description of the corals of the Qahlah and Simsima Formations.

STUDY AREA

The study area lies along the border between the United Arab Emirates and the Sultanate of Oman (Fig. 1). The corals were collected from outcrops, comprising outlying jebels (hills) along the western fringes of the Oman Mountains (Figs 2–4): **Jebel Huwayyah**, 10 km NE of Al Ain; **Jebel Bu Milh**, ca. 40 km NE of Al Ain; **Jebel Rawdah**, east of Al Madam; **Jebel Buhays**, 4 km north of Al Madam; **Jebel Thanais**, 4 km north of Al Madam; **Jebel Faiyah**, north of Al Madam, and **Qarn Murrah**, 15 km north of Al Madam. Detailed information on the sections logged and studied are given in Smith *et al.* (1995a).



Fig. 1 Map of the Arabian Peninsula showing the area of study.



Fig. 2 Locality map showing the position of the four major jebels (hills) studied (asterisked) where there are important outcrops of late Cretaceous sediments.

STRATIGRAPHY

The Upper Cretaceous to Lower Palaeocene rocks of the Oman Mountains area of the United Arab Emirates-Oman border area are divided into three units (Skelton *et al.*, 1990):

3. The **Pabdeh Group** – a basal limestone conglomerate of re-worked Simsima Formation with an erosive base of presumably early Palaeocene age, overlain by thin-bedded basinal marls of late Palaeocene age.
2. The **Simsima Formation** – a platform carbonate sequence of Maastrichtian age.
1. The **Qahlah Formation** – a marine clastic sequence of sands and conglomerates of late Campanian or early Maastrichtian in age.

Combining the evidence from ammonites, inoceramid bivalves,

echinoids and global sea-level curves Smith *et al.* (1995a) concluded that the basal beds of the Qahlah Formation are of latest Campanian age. At Jebel Huwayyah, the *Loftusia*-rich levels of the Qahlah Formation probably encompass Lower to early Upper Maastrichtian. The Simsima Formation appears to be early Upper Maastrichtian, *fresvillensis* Zone or later.

SYSTEMATIC DESCRIPTIONS

Abbreviations for the dimensions in the text are as follows: **d** = corallite diameter; **d (*)** = corallite diameter recorded in less than 10 % of the calices in the same individual; **d (max)** = maximum calicular diameter; **d (min)** = minimum calicular diameter; **dl** = diameter of lumen; **c–c** = distance between centres of calices; **c–c (series)** = distance between centres of the same calicinal series; **c–c (series): (n)** = distance between centres of the same calicinal series occurring in less than 10% of the measurements in the same individual; **s** = number of septa; **s (*)** = number of septa occurring in less than 10% of the corallites of the same individual; **s/mm** = density of septa measured on ridges or outer calicinal regions, if not indicated otherwise; **h** = height of corallum, note that the terms **cycles** and **orders** of septa are used in the sense that septa of the same cycle belong to a single stage in ontogeny, septal orders refer to the different sizes of septa; the notation **S1, S2**, etc. refers to either cycles or orders; **(st)** = height of corallum from stem to upper surface; **(e)** = height of corallum from the extremities to upper surface.

Note that microstructural features are not preserved, if not indicated otherwise in the descriptions. The terms **minitrabeculae**, **medium-sized trabeculae** and **thick trabeculae** are used in the sense proposed by Morycowa & Roniewicz (1995a), according to which minitrabeculae are up to 50 µm in size, medium-sized trabeculae measure 50 to 100 µm, and thick trabeculae are over 100 µm in size. **Centres of calcification** are used in that due to the poor preservation the size of the trabeculae cannot be identified. In cases where the axial structures '**pali**' and '**paliform lobes**' cannot be distinguished they have simply been referred to in the taxonomic description as '**paliform structures**'.

The coral classification for the genera used herein is a combination of several different models: taxonomic levels organized by Vaughan & Wells (1943) concern the suborders Faviina, Dendrophylliina, Caryophylliina, Fungiina, and the families Faviidae, Montlivaltiidae, Dendrophylliidae, Haplaraeidae, Poritidae, Actinacidae and Caryophylliidae. Later modifications by Alloiteau (1952a) concern the suborders Archaeocoeniina, Stylinina, Meandriina, and the families Actinastreaeidae, Stylophoridae, Heliastreaeidae, Columastreaeidae, Placocoeniidae, Placosmiliidae, Isastreaeidae, Dendrogyridae, Meandriidae, Andemantastraeidae and Parasmiliidae. Further changes in the coral classification are due to the works by L. & M. Beauvais (1975) for the family Agatheliidae; Roniewicz (1976) for the suborder Rhipidogyrina, and the families Rhipidogyridae and Dermosmiliidae; Morycowa & Roniewicz (1990) for the family Cladophylliidae; Morycowa & Roniewicz (1995b) for the suborder Microsolenina, and the families Latomeandriidae and Cunnilitidae; and Baron-Szabo (herein) for the family Brachyphylliidae.

The material is deposited at the Department of Palaeontology, The Natural History Museum, London, and registration numbers have the prefix AZ.

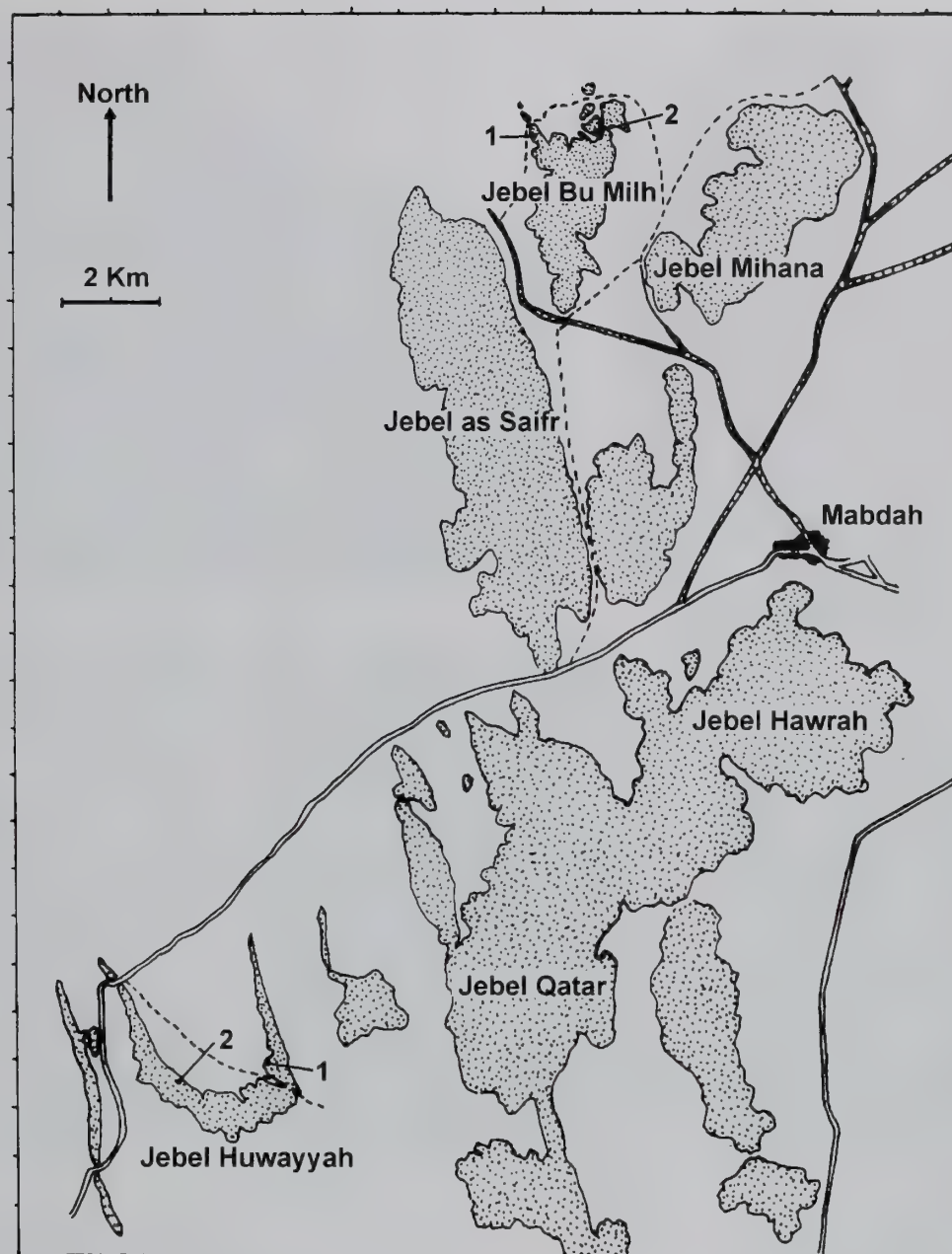


Fig. 3 Detailed locality map for Jebel Huwayyah and Jebel Bu Milh.

Class **ANTHOZOA** Ehrenberg, 1834

Subclass **ZOANTHARIA** Blainville, 1830

Order **SCLERACTINIA** Bourne, 1900

Suborder **ARCHAEOCOENIINA** Alloiteau, 1952

Family **ACTINASTREIDAE** Alloiteau, 1952

Genus **ACTINASTREA** d'Orbigny, 1849

TYPE SPECIES. *Astrea geminata* Goldfuss, 1826.

Actinastrea bastidensis Alloiteau, 1954 Pl. 1, fig. 2

*1954 *Actinastrea bastidensis* Alloiteau: 84–87, pl. III, fig. 4, pl. X, fig. 4.

v1998 *Actinastrea bastidensis* Alloiteau; Baron-Szabo: 129, pl. 1, fig. 5.

MATERIAL. AZ 48; AZ 639 (two specimens).

MEASUREMENTS. d: (*1.2) 1.5–2.2 mm; c–c: 1.5–2.2 mm; s: 24 (*+s4); size of the colony: domal shaped: 7 cm in height, with a varying diameter of about 4 to 5 cm; knobby: 2.5–4 cm in diameter.

DESCRIPTION. Massive-domal, or knobby, cerioid corallum with calices that are directly united by their walls. Corallites are poly-

gonal in outline. Gemmation is due to extracalicular and to a lesser extent intracalicular budding. Costosepta are compact, nonconfluent or subconfluent, and arranged in 3 cycles in 6 systems, radially and bilaterally. Septa of the first cycle extend to, and may fuse with, the columella. Septa of the second cycle are nearly of the same length, but distinctly thinner. Septa of the third cycle regularly alternate with the second cycle septa. In some calices the beginning of a fourth cycle is present. Lateral surfaces of the septa are covered with spiniform and rounded granules. The columella is styliform. The wall is septothecal with lacunae. Endothecal dissepiments are thin and vesicular. Microstructure is poorly preserved, but in places minor or medium-sized centres of calcification are present.

OCCURRENCE. Simsim Formation, lowest 2 m, Jebel Faiyah, 5 km north of Al Madam; outcrop on the east face, ca. 3 km north of the southern tip of Jebel Faiyah, NNE of Al Madam.

DISTRIBUTION. Upper Santonian of southern France (Corbières), Campanian of northern Spain (Catalonia).

Actinastrea ramosa (Michelin, 1847) Pl. 1, fig. 3

*1847 *Astrea ramosa* Michelin: 303, pl. 72, fig. 4.

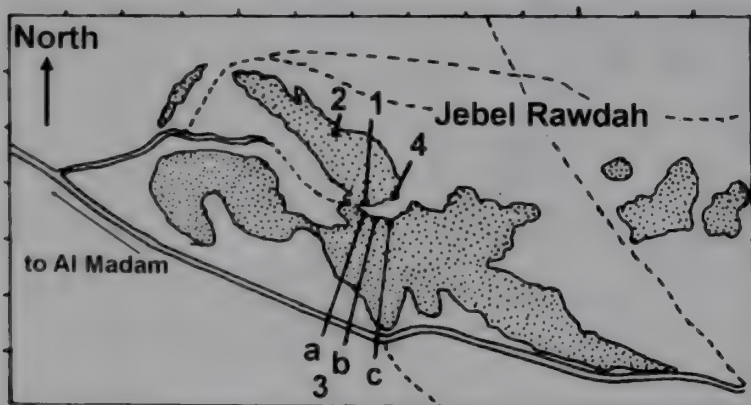
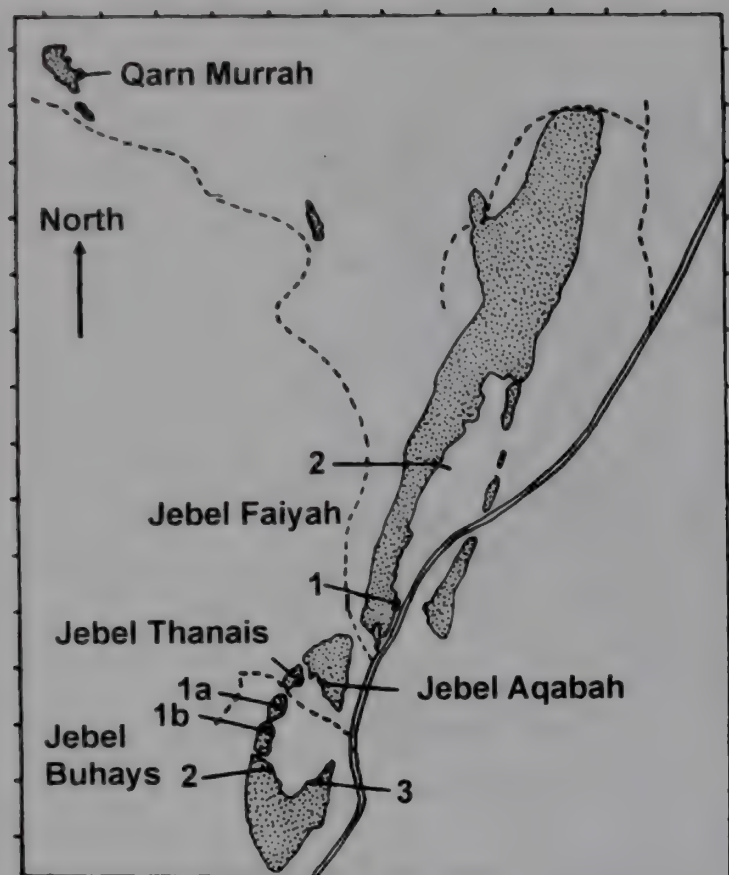


Fig. 4 Detailed locality map for Qarn Murrah and Jebels Buhays, Thanais, Aqabah and Faiyah (upper), and Jebel Rawdah (lower).

1848 *Astrocoenia ramosa* (Michelin); Milne Edwards & Haime: 298.

1861 *Astrocoenia ramosa* (Michelin); Fromentel: 233.

1954 *Actinastrea ramosa* (Michelin); Alloiteau: 53, pl. IV, fig. 3, pl. VIII, fig. 3.

?1956 *Astrocoenia ramosa* (Michelin); Bendukidze: 114.

1978 *Actinastrea ramosa* (Michelin); Turnšek, in Turnšek & Polšak: 145, 166, pl. 1, figs 1–3.

1982 *Actinastrea ramosa* (Michelin); Beauvais, tome I: 16 (older synonyms cited therein).

1989 *Actinastrea ramosa* (Michelin); Löser: 96, text-fig. 1.

1994 *Actinastrea ramosa* (Michelin); Turnšek: 9, pl. 1, figs 5–6.

1997 *Actinastrea ramosa* (Michelin); Löser: 79, pl. 1, fig. 1.

MATERIAL. AZ 365; AZ 662; AZ 896.

MEASUREMENTS. d: (*0.8) 1–1.3 mm; c–c: 0.9–1.5 mm; s (adult): 16 (8s₁+8s₂), s (juvenile): 10 (5s₁+5s₂) – 12 (6s₁+6s₂); size of the colony: 6–11 cm in diameter.

DESCRIPTION. The corallum forms a massive and cerioid colony with corallites united by their walls. Calices are polygonal in outline. Gemmation is due to intra- and extracalicular budding. Costosepta are compact, non- or sub-confluent, finely granulated on their lateral surfaces, 16 in number, which are arranged in 2 orders in 8 systems. Septal development in five or six systems is present in juvenile corallites. Septa of the first order extend to, and may fuse with, the columella. Septa of the second order are distinctly thinner, reaching about half the length of the oldest ones. The columella is styliiform. Wall is septothecal with lacunae. The endotheca consists of very thin vesicular or subtabulate dissepiments.

REMARKS. The occurrence of septal arrangements in the juvenile stage differing from the ones in the adult stage indicates an inconsistency in the ontogenetical development of the septal apparatus. Therefore, the septal arrangement corresponds to size orders rather than to cycles.

OCCURRENCE. *Loftusia* Bed (beds 3–8), SW corner of Jebel Huwayyah, east of Al Ain; east face of northern hill forming Jebel Buhays, 4 km north of Al Madam; from bed 19 north side of valley, 2 km east of Jebel Rawdah, east of Al Madam.

DISTRIBUTION. Upper Cenomanian of Germany (Saxony), ?Senonian of Georgia (in Caucasia) and Hungary, Coniacian-Campanian of Austria (Gosau Group), Santonian-Campanian of Slovenia, Upper Santonian of southern France (Corbières) and northern Spain (Catalonia), Campanian of Turkey.

Actinastrea elongata Alloiteau, 1954

Pl. 1, fig. 6

*1954 *Actinastrea elongata* Alloiteau: 41, pl. I, fig. 10, pl. VII, fig. 4.

MATERIAL. AZ 208; AZ 571; AZ 905; 3.4X.

MEASUREMENTS. d (max): (*1.8) 2.2–3 mm; d (min): 1.5–2.2; c–c: 1.5–3 mm; s: 20 (10s₁+10s₂); size of the colony: about 15 cm in diameter.

DESCRIPTION. Massive colony with corallites that are polygonal or slightly rounded in outline. Gemmation is due to extracalicular and intracalicular budding. Costosepta are compact, straight, developed

PLATE 1

Micrographs of plocoid (1, 7) and cerioid (2–6) coral colonies from transverse thin-sections and upper surface views.

Figs 1, 7 *Stylophora octophylla* (Felix, 1906); 1, AZ 560; 7, AZ 548.

Fig. 2 *Actinastrea bastidensis* Alloiteau, 1954; AZ 639.

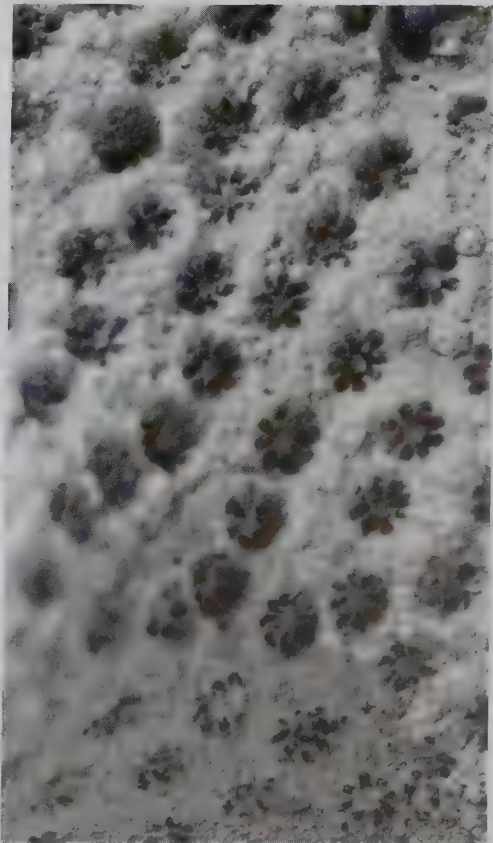
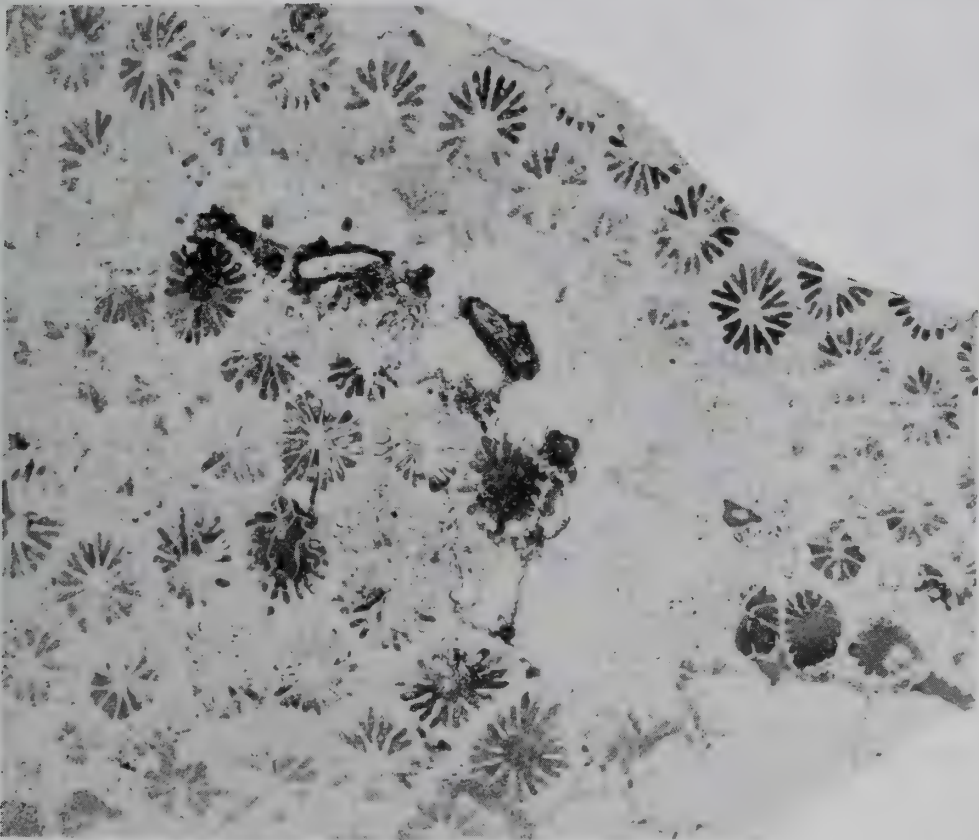
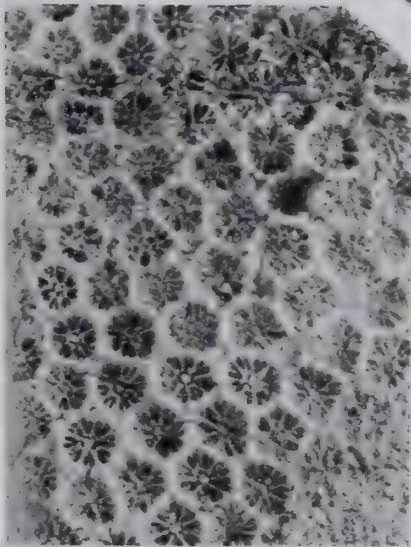
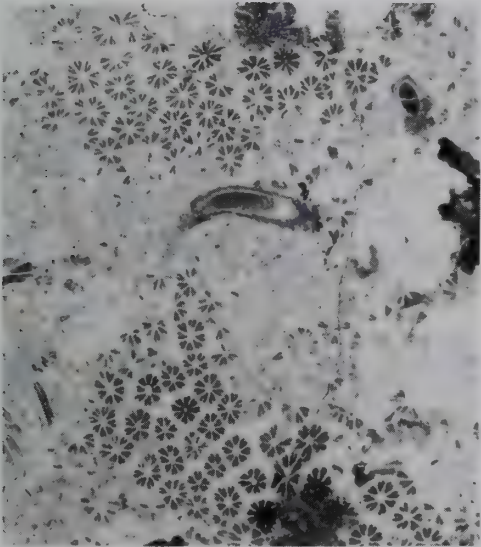
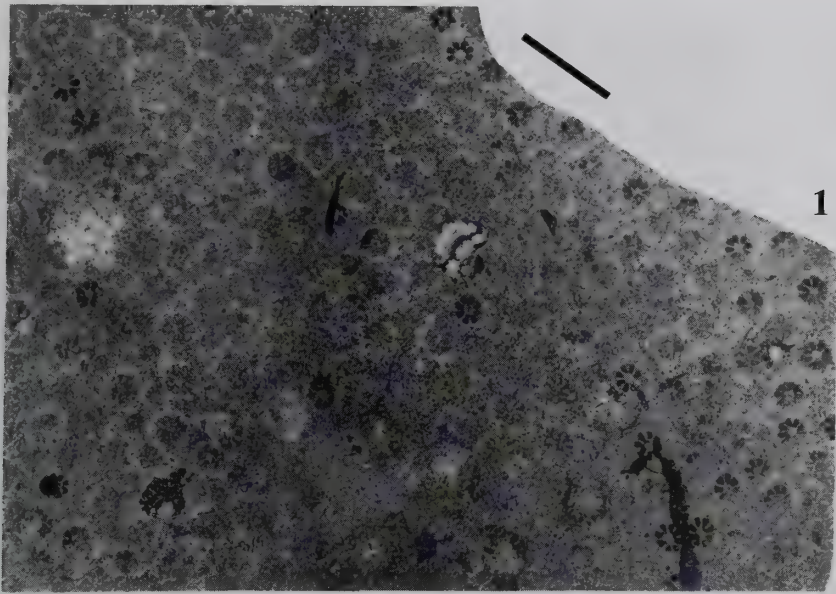
Fig. 3 *Actinastrea ramosa* (Michelin, 1847); AZ 365.

Fig. 4 *Columactinastraea pygmaea* (Felix, 1903); AZ 471.

Fig. 5 *Columactinastraea guadelupae* (Wells, 1932); AZ 2539.

Fig. 6 *Actinastrea elongata* Alloiteau, 1954; AZ 905.

Scale bar = 3 mm.



in 2 complete cycles in 10 systems, and have delicate spiniform granules laterally. In general, septa of the first cycle extend to the centre of the calice where their inner ends may merge with the columella. Septa of the second cycle are distinctly shorter, reaching about one-quarter the length of the oldest ones. The columella is styliiform or substyliiform, well-developed. Wall is septothecal with rare pores. Endotheca consists of a small number of thin, subtabulate dissepiments. Septal microstructure is made of simple medium sized trabeculae, sometimes producing ?lateral trabeculae.

OCCURRENCE. Qahlah Formation, *Loftusia* beds, SW corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Maastrichtian of France.

Genus *COLUMACTINASTRAEA* Alloiteau, 1952

TYPE SPECIES. *Columactinastraea rennensis* Alloiteau, 1952.

Columactinastraea pygmaea (Felix, 1903)

Pl. 1, fig. 4, Pl. 2, fig. 4

- *1903b *Astrocoenia pygmaea* Felix: 54, pl. 3, figs 4–5.
 1914 *Astrocoenia pygmaea* Felix; Felix, pars 7: 235.
 1954 *Actinastrea pygmaea* (Felix); Alloiteau: 52, pl. IV, fig. 6, VIII, fig. 2.
 1975 *Actinastrea pygmaea* (Felix); Beauvais *et al.*: 44, pl. IV, figs 1a, b.
 1978 *Columactinastraea pygmaea* (Felix); Turnšek, *in* Turnšek & Polšak: 147, 168, pl. 3, figs 1–4.
 1994 *Columactinastraea pygmaea* (Felix); Turnšek: 9, pl. 2, figs 1–3.
 1997 *Columactinastraea pygmaea* (Felix); Turnšek: 39, figs 39A–C.
 v1998 *Columactinastraea pygmaea* (Felix); Baron-Szabo: 130, pl. 2, fig. 1.

MATERIAL. AZ 213; AZ 471; AZ 537; AZ 541; AZ 553; AZ 555; AZ 558; AZ 928.

MEASUREMENTS. d: (*0.9) 1.1–1.7 mm; c–c: (*1) 1.3–2.2 mm; s: 8s1+8s2 (*+s3); size of the colony: 2.5–10 cm in diameter.

DESCRIPTION. The corallum is massive-knobby and cerioid with calices which are polygonal or slightly rounded in outline. Costosepta are arranged in two complete cycles in 8 systems. In some calices the beginning of a third cycle is visible. Septa of the first two cycles can be subequal or regularly alternating in length and thickness. Youngest septa are distinctly thinner and shorter. Septa are compact and non- or subconfluent. Their lateral surfaces have numerous delicate granulations. Paliform structures irregularly occur in front of first and second cycle septa. The columella is styliiform or consists of a few papillae, sometimes fusing with one of the oldest septa. The wall is septothecal with rare pores. The endotheca is made of vesicular dissepiments.

OCCURRENCE. Main Gastropod Level (beds 7/8), north side of Jebel Bu Milh, 25 km NE of Hili; *Loftusia* Beds, Qahlah Formation,

SE corner of Jebel Huwayyah, east of Al Ain; outcrop at southern tip of Jebel Faiyah (lowest 3 m of section), 6 km NNE of Al Madam.

DISTRIBUTION. Santonian-Campanian of southern France, Slovenia, and Croatia, Campanian of Portugal.

Columactinastraea guadelupae (Wells, 1932) Pl. 1, fig. 5

- v*1932 *Stephanocoenia* (?) *guadelupae* Wells: 235, pl. 32, figs 8, 9, pl. 39, fig. 3.
 1944 *Stephanocoenia guadelupae* Wells; Wells: 433, pl. 69, figs 3,4.
 v1998 *Columactinastraea guadelupae* (Wells); Baron-Szabo: 130, pl. 2, fig. 1.

MATERIAL. AZ 483; AZ 504; AZ 900; AZ 907–13; AZ 915; AZ 919–22; AZ 933–34; AZ 2536; AZ 2539.

MEASUREMENTS. Comparison of the dimensions (in mm) of skeletal elements of the specimens from UAE/ Oman (here), Spain (Baron-Szabo, 1998) and Texas (Wells, 1932).

	UAE/Oman	Spain	Texas
d:	2–4	(2,5) 3–4,5	2,,5–4
dl:	(*1.5) 2–2.5	1,8–2,5	1,7) 2,2
c–c:	2–4	3–4,5	(not stated)
s:	(22) 24	(20) 24	24

*size of the colony = 3–11 cm in diameter.

DESCRIPTION. The corallum is a massive, nodular or lamellar colony with calices which are rounded or subpolygonal in outline. Costosepta are arranged in three complete cycles in 6 systems, irregularly alternating in length. They are compact, non- or subconfluent and have spiniform granules laterally. Septa of the first and second cycle can be of the same thickness. Their inner ends have separate pali that appear to form a ring of 8–12 around the columella. The columella is styliiform or substyliiform. Third cycle septa are very short, appearing as small thorns. The wall is a well-developed septotheca with rare pores. The endotheca consists of vesicular or subtabulate dissepiments.

REMARKS. The specimens from the UAE/ Oman closely correspond to both the type and the material from Spain.

OCCURRENCE. Qahlah Formation (beds 10/ 11, above level of 1st ammonite *Loftusia* beds, and coral clast horizon), SE corner of Jebel Huwayyah, east of Al Ain; NW end of Jebel Milh, 25 km NE of Hili.

DISTRIBUTION. Upper Aptian-Lower Albian of Venezuela (Barranquin Formation), Middle Albian of Texas, Campanian of northern Spain (Catalonia).

Family **STYLOPHORIDAE** Milne Edwards, 1857

Genus *STYLOPHORA* Schweigger, 1819

TYPE SPECIES. *Madrepora pistillata* Esper, 1792.

PLATE 2

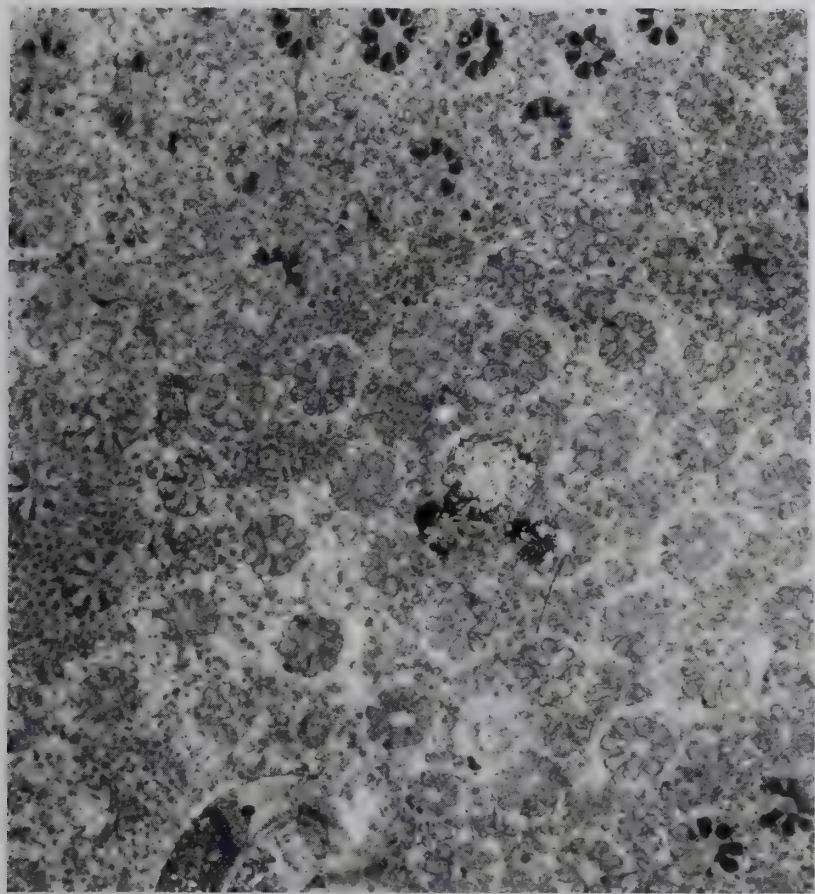
Micrographs of plocoid (1, 2), cerioid (4), and (hydno-phoro-) meandroid (3, 5) coral colonies in cross and transverse thin-sections.

Figs 1, 2 *Stylophora octophylla* (Felix, 1906); AZ 560.

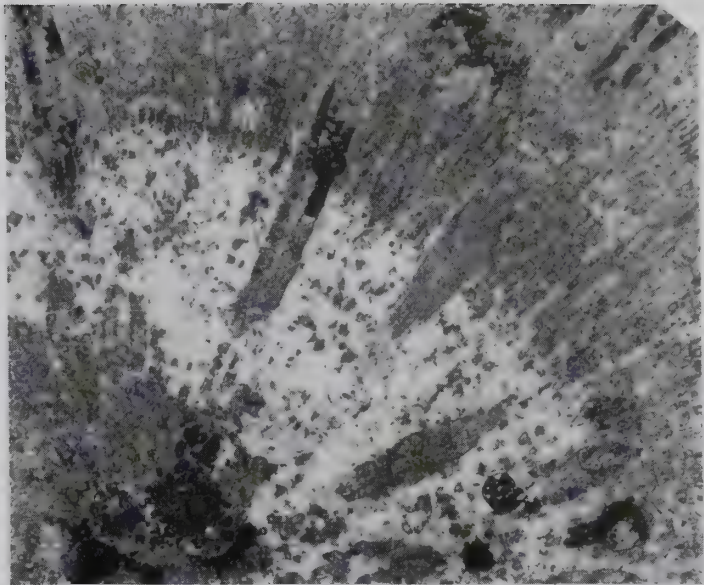
Figs 3, 5 *Monticulastraea insignis* Duncan, 1880; AZ 74.

Fig. 4 *Columactinastraea pygmaea* (Felix, 1903); AZ 541.

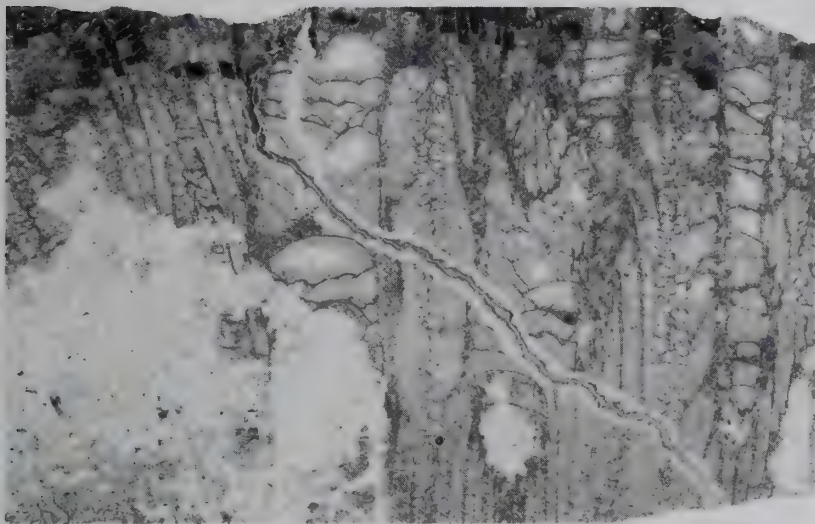
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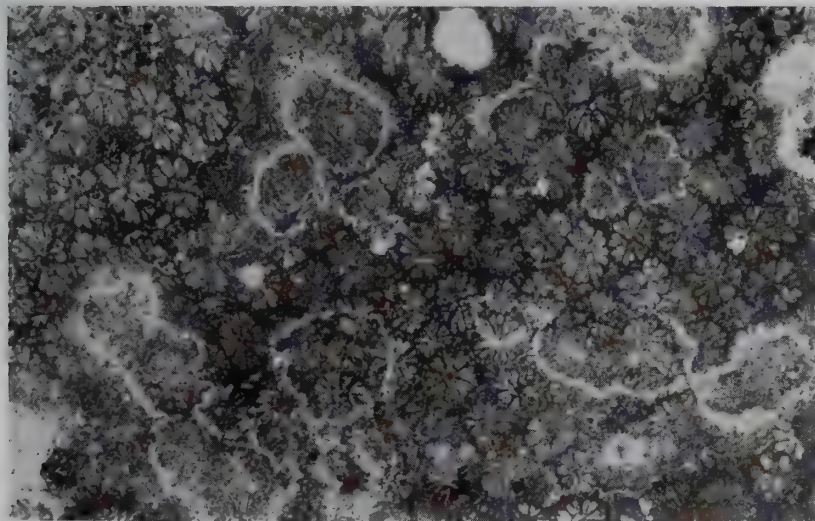
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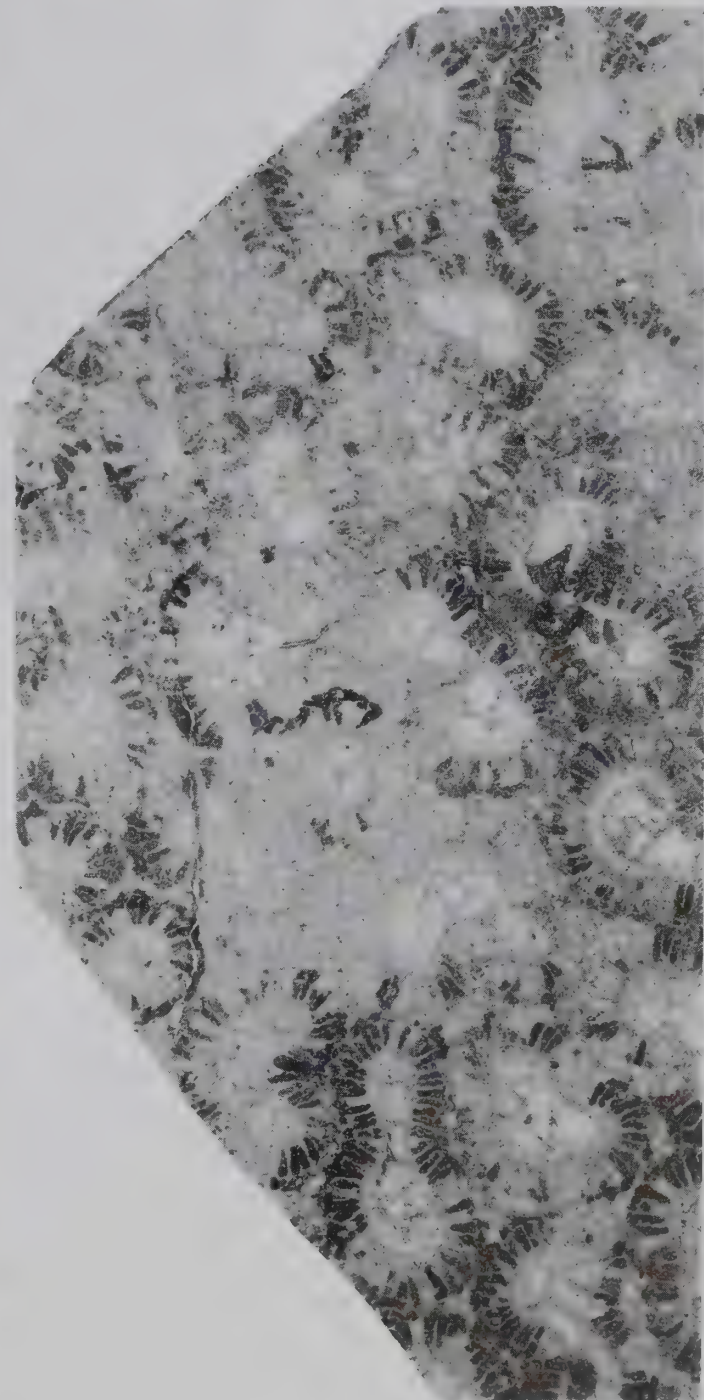
2



3



4



5

Stylophora octophylla (Felix, 1906)

Pl. 1, figs 1, 7, Pl. 2, figs 1, 2

*1906 *Astraeaopora octophylla* Felix: 44, pl. III, figs 6, ?6a.1911 *Actinacis* (?) *octophylla* (Felix); Trauth: 161.

MATERIAL. AZ 405; AZ 458; AZ 524; AZ 526; AZ 538; AZ 544; AZ 548; AZ 552; AZ 557; AZ 559; AZ 560.

MEASUREMENTS. d: 0.6–1.1 mm; c–c: 1–2.5 mm; s: 8 (*+s2); size of the colony: 2–10 cm in diameter.

DESCRIPTION. The corallum is irregularly massive or ramose and plocoid, with calices that are separated by a dense, granular coenosteum. Gemmation is due to extracalicular budding. Corallites are circular in outline. Costosepta are straight, nonconfluent, compact, and arranged in 1 cycle in 8 systems. In some calices a septal development in ?6 or ?7 systems is present. Septa might extend to, and fuse with, the columella. In a few calices the beginning of a second cycle can be observed. Septal flanks are covered by very delicate spiniform granules. Columella is styliform. Synapticulae are scattered throughout the colony. The wall is parathecal and synapticulothecal, with pores. Endotheca consists of numerous thin, subtabulate or slightly arched dissepiments. Exotheca is made of vesicular dissepiments.

REMARKS. In the specimen described by Felix (1906) the development of the trabecular and sponge-like coenosteum, together with the appearance of both an incomplete wall and a (?pseudo-) columella, suggests that it represents a form of *Stylophora* Schweigger. (Original description in Felix 1906: 44: '... Das Gewebe der Koralle besteht aus einem trabekulären Coenenchym, dessen einzelne Bälkchen durch querleistenartige Verdickungen und Synaptikeln verbunden werden. Die Oberfläche erscheint wie mit feinen, wirren Runzeln bedeckt bzw. hat eine große Ähnlichkeit mit dem Gewebe vieler Spongien. In diesem Coenenchym zerstreut liegen nun zahlreiche, kleine, rundliche Kelche. Ihre Mauer scheint nie kompakt zu werden, sondern stets unvollständig zu bleiben. Ihr Durchmesser beträgt meist 1 mm. In ihnen sieht man gewöhnlich 8 Septen, welche im Mittelpunkt zusammenzustößen pflegen, wodurch eine Art Pseudokolumella entsteht ...').

OCCURRENCE. *Loftusia* Level (Beds 3–8), SW corner of Jebel Huwayyah, east of Al Ain; outcrop at southern tip of Jebel Faiyah (lowest 3 m of section, bed 2, base of bed 6), 6 km NNE of Al Madam; outcrop on east face, ca. 3 km north of the southern tip of Jebel Faiyah, NNE of Al Madam; loose from lowest 3–4 m of section at east face of most northern hill forming Jebel Buhays (beds 4–11), 4 km north of Al Madam.

DISTRIBUTION. Senonian of Slovakia and Romania.

Suborder FAVIINA Vaughan & Wells, 1943

Family FAVIIDAE Gregory, 1900

Subfamily FAVIINAE Vaughan & Wells, 1943

REMARKS. The systematic position of the genus *Monticulastraea*

Duncan has been discussed since the last century. Felix (1914) does not record it in his Fossilium Catalogus, Vaughan & Wells (1943) and Wells (1956) conceive this genus as a younger synonym of *Hydnophora* Fischer von Waldheim, Alloiteau (1952a, 1957) does not document this form, Gregory (1930) gives a short review of *Monticulastraea* and designates the type species. Recently, Bosellini (1999) compared Tertiary representatives of *Monticulastraea* Duncan and *Hydnophora* Fischer von Waldheim. She concluded that the skeletal elements in both forms are nearly identical, and therefore suggested that they are synonymous. However, the specimens at hand distinctly differ from Bosellini's model in that they have monticules consisting of coenosteum with large vesicular dissepiments forming an exothecal wall. The development of such skeletal structures exclude the forms from the genus *Hydnophora*, and supports the idea that *Monticulastraea* is not congeneric with *Hydnophora*. It seems necessary to investigate and compare more of those specimens from both Cretaceous and Tertiary strata to evaluate the pertinent taxonomical criteria (Bosellini & Baron-Szabo, in prep.).

The specimens from the UAE/ Oman closely agree with the generic conception by Duncan (1880), Gregory (1930), and Kühn (1933).

Genus *Monticulastraea* Duncan, 1880TYPE SPECIES. *Monticulastraea elongata* Duncan, 1880.*Monticulastraea insignis* Duncan, 1880

Pl. 2, figs 3, 5, Pl. 5, fig. 3

*1880 *Monticulastraea insignis* Duncan: 87, pl. XXVI, figs 1–3.1930 *Monticulastraea insignis* Duncan; Gregory: 96.1933 *Monticulastraea insignis* Duncan; Kühn: 194.

MATERIAL. AZ 62; AZ 74–75; AZ 84; AZ 294–97; AZ 461; AZ 540; AZ 656; AZ 2538.

MEASUREMENTS. d (series): 1.5–5 mm; maximum diameter of monticules: 2–9 mm; minimum diameter of monticules: 0.5–3 mm; s/mm: 7–11/2; size of the colony: 6.5–12 cm in diameter.

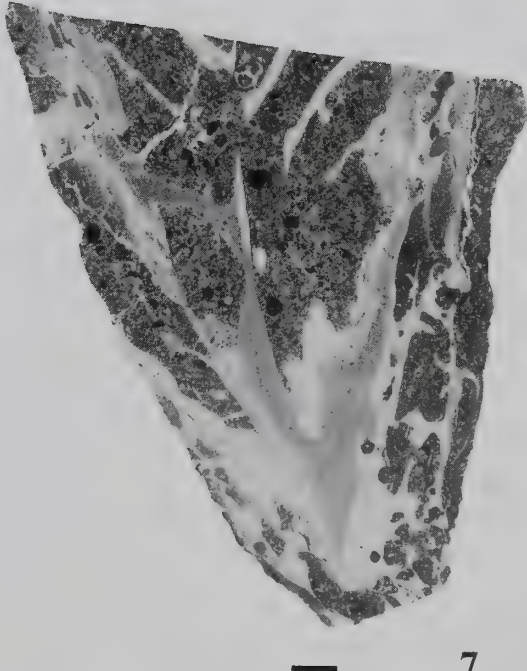
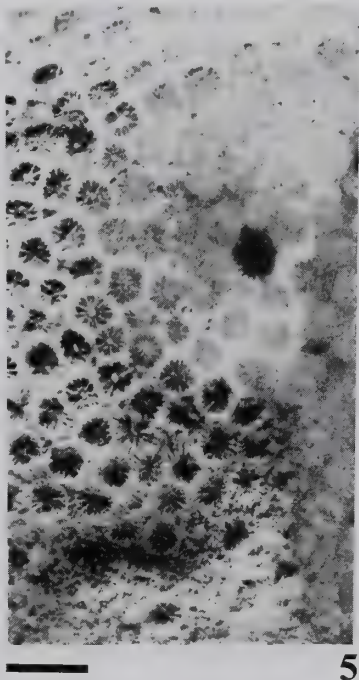
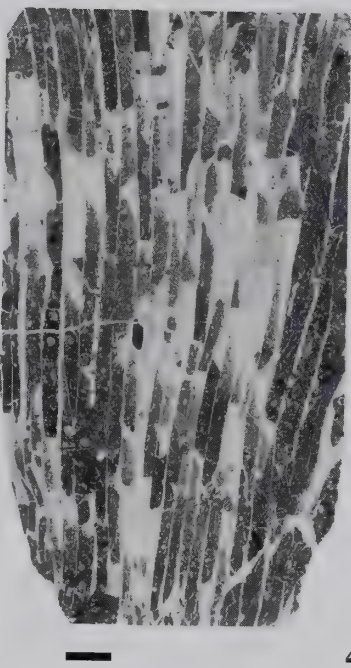
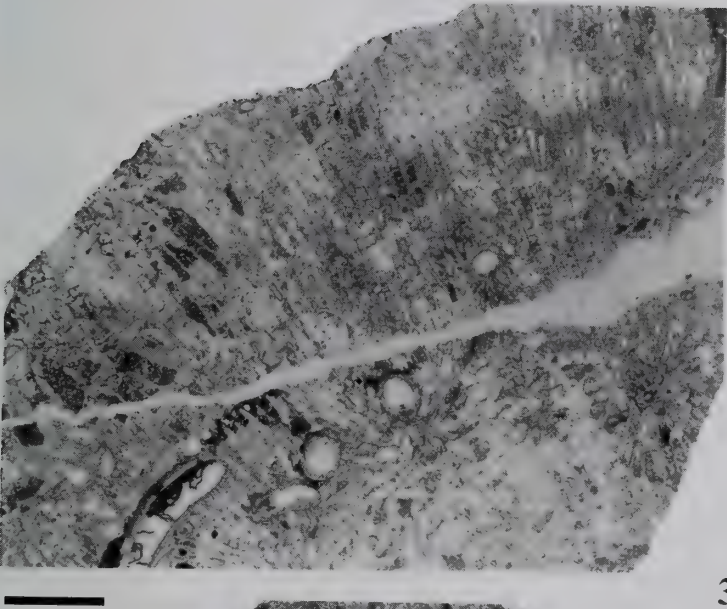
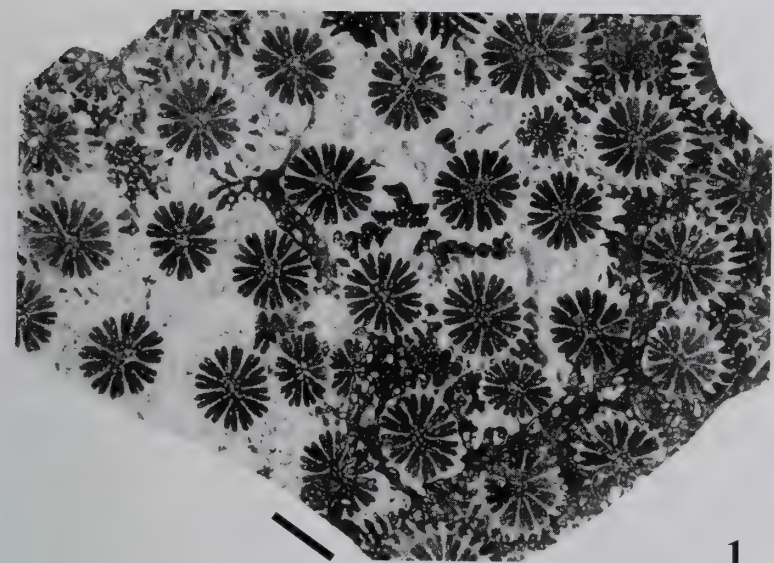
DESCRIPTION. The corallum is massive with corallites that are arranged in sinuous series defined by short tectiform monticules, consisting of coenosteum. Costosepta are compact, thin, straight, and arranged in two with a beginning third size orders. Septa of the first two orders extend to the centre of the series where their inner ends terminate in claviform thickenings or fuse with the columella. They slightly alternate in thickness. Septa of the third order are distinctly shorter and thinner. Septal flanks are covered with delicate spiniform granules. Columella is lamellar, thin, and continuous. The wall is septothecal. Endotheca consists of thin, tabulate or slightly arched dissepiments. Exotheca is made of large vesicular dissepiments. The microstructure is formed by simple minitraculae sometimes giving off secondary ones (septa), and simple or polyaxial minitraculae (wall).

PLATE 3

Micrographs of plocoid (1, 3, 5, 6) and turbinate (2, 4, 7) coralla in transverse and longitudinal thin-sections, and upper surface view.

Fig. 1 *Neocoenia lepida* (Reuss, 1854); AZ 479.Figs 2, 4, 7 *Montilivaltia* sp.; AZ 57.Figs 3, 6 *Stephanaxophyllia casterasi* Alloiteau, 1957; AZ 456.Fig. 5 *Columastrea dubia* Alloiteau, 1958; AZ 47.

Scale bar = 3 mm.



REMARKS. The specimens from the UAE/ Oman very closely agree with the description and illustration of the type material. The type species was designated by Gregory (1930: 96).

OCCURRENCE. Outcrop on east face, ca. 3 km north of southern tip of Jebel Faiyah, NNE of Al Madam; outcrop forming slope and cliff on north side of Jebel Bu Milh, 25 km NE of Hili (beds 3/4); east face of most northern hill forming Jebel Buhays, 4 km north of Al Madam; outcrop on south side of slope, 3 km east of Jebel Rawdah, east of Al Madam; outcrop at southern tip of Jebel Faiyah (base of bed 6), 6 km NNE of Al Madam.

DISTRIBUTION. Burdigalien-Upper Miocene of India (base of Gáj Group).

Family **HELIASTREIDAE** Alloiteau, 1952

Genus **NEOCOENIA** Hackemesser, 1936

TYPE SPECIES. *Neocoenia renzi* Hackemesser, 1936.

Neocoenia lepida (Reuss, 1854) Pl. 3, fig. 1

*1854 *Astrea lepida* Reuss: 114, pl. XII, figs 1, 2.

v1903a *Phyllocoenia lepida* (Reuss); Felix: 293.

1936 *Phyllocoenia lepida* (Reuss); Hackemesser: 19.

1978 *Neocoenia lepida* (Reuss); Turnšek, in Turnšek & Polšák: 153, 172, pl. 10, figs 1–3.

v1997 *Neocoenia lepida* (Reuss); Baron-Szabo: 64, pl. 5, figs 3, 4 (older synonyms are cited therein).

MATERIAL. AZ 413–14; 451; AZ 453; AZ 470; AZ 479; AZ 638; AZ 658; AZ 923; AZ 931.

MEASUREMENTS. d (lumen): 2.5–4 (*4.5) mm, juvenile: 1.5–2 mm; d: 3.5–4.5 (*5.5) mm, juvenile: 2.5 mm; c–c: (*3) 3.5–6.5 mm; s: 24 +s3, juvenile: 20; size of the colony: 5–13 cm in diameter.

DESCRIPTION. The corallum is in the form of a massive, plocoid colony with corallites that are circular in outline. Calices are regularly disposed on the surface of the colony. Costosepta are straight,

nonconfluent, compact, 24 in number, and arranged in three cycles and 6 systems. They regularly alternate in length. Septal flanks have spiniform granulations. Septa of the first cycle extend to, and may fuse with, the columella. The inner ends of first and second cycle septa can be slightly swollen. Paliform structures irregularly occur in front of S_1 and S_2 . Intercorallite areas are crossed by the costae when corallites are close together; when they are more distant, costae merge into a porous, reticulated coenosteum. The columella is variably developed: spongy-papillose, thin lamellar, or formed by a few twisted segments. The wall is parathecal, in places septoparathecal. Endotheca consists of thin vesicular or subtabulate dissepiments. Septal microstructure consists of simple mini- or medium-sized trabeculae.

REMARKS. According to Hackemesser (1936) the material from central Greece he investigated was determined as Cenomanian in age. Due to recent studies of the rudists at the same locality carried out by Th. Steuber, Erlangen, (pers. comm.) these deposits possibly represent a mixture of stratigraphically heterogeneous sediments (Aptian to Campanian). Therefore, in chapter on distribution mentioned here the age of the locality in Hackemesser (1936) is accompanied by a question mark (previously discussed in Baron-Szabo, 1998).

OCCURRENCE. Outcrop forming slope and cliff on north side of valley (beds 3, 10), 3 km east of Jebel Rawdah, east of Al Madam; SW corner of Jebel Huwayyah, east of Al Ain; east face of most northern hill forming Jebel Buhays, 4 km north of Al Madam; loose, derived from 3–4 m of section NE side of Jebel Buhays, 4 km north of Al Madam; Qahlah Formation, loose from *Loftusia* Beds, SE corner of Jebel Huwayyah, east of Al Ain; outcrop on east face, ca. 3 km north of the southern tip of Jebel Faiyah, NNE of Al Madam.

DISTRIBUTION. Cenomanian-Turonian of France, Cenomanian of Lebanon, ?Cenomanian of Greece, ?Upper Turonian-Lower Coniacian and Santonian-Campanian of Austria (Gosau Group), Santonian-Campanian of Hungary and Romania, Campanian of Serbia.

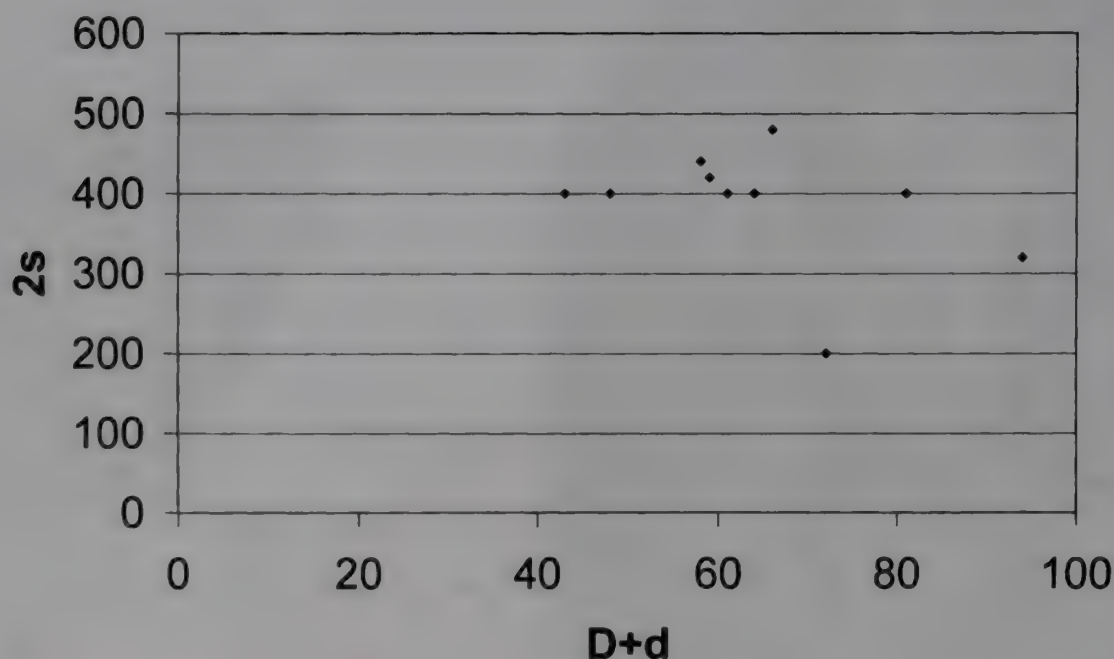


Fig. 5 Ratio of number of septa (2s) to the average diameter (D+d) for the specimens of *Montlivaltia* sp. The points are widely scattered suggesting that the population consists of several species.

Family **MONTLIVALTIIDAE** Dietrich, 1926
Genus **MONTLIVALTIA** Lamouroux, 1821

TYPE SPECIES. *Montlivaltia caryophyllata* Lamouroux, 1821.

REMARKS. The validity of species of *Montlivaltia* Lamouroux has been discussed for several decades (e.g. Lambelet, 1968; Turnšek, 1972; Errenst, 1990). According to studies on Upper Jurassic forms of *Montlivaltia* carried out by Lambelet (1968) the characteristics which have been used to establish new taxa are directly dependent on ecological features (e.g. deep or shallow calice: agitated or quiet water; shape of the corallum: soft or hard substrate, sedimentation rate, water movement). It seems necessary to revise the group and evaluate the pertinent taxonomical criteria. Therefore, the specimens here are not assigned to any species (see Fig. 5).

Montlivaltia sp. Pl. 3, figs 2, 4, 7

MEASUREMENTS. Dimensions of skeletal elements of the specimens of *Montlivaltia*.

	D (max) mm	d (min) mm	d/D	h mm	s
AZ 57	59	35	0.59	50	160
AZ 79	46	35	0.76	30	200
AZ 481	42	30	0.71	65	100
AZ 71	40	24	0.60	55	200
AZ 33	37	29	0.78	25	240
AZ 80	36	25	0.70	30	200
AZ 54	35	24	0.69	35	210
AZ 68	30	28	0.93	45	220
AZ 78	27	21	0.78	30	200
AZ 83	27	16	0.59	25	200

DESCRIPTION. The corallum is turbinate, ceratoid, cuneiform, or trochoid, elliptical or nearly circular in outline. Septa are compact, thin, straight, and arranged in 5 complete cycles with the beginning of a sixth cycle, in 6 systems. Septa of the first two cycles can be nearly equal in length and thickness. They reach the centre of the corallite, circumscribing the calicular pit. Remaining cycles of septa regularly alternate in length and thickness. Septal flanks are covered by delicate rounded granules, frequently forming carinae. There is no columella. Endothecal dissepiments are numerous, subtabulate or vesicular. Microstructure is poorly preserved, but in places simple minitrabeculae, and compound mini- or medium-sized trabeculae are present.

OCCURRENCE. *Loftusia* Level, main coral bed (beds 3–8), SW corner of Jebel Huwayyah, east of Al Ain.

MATERIAL. See Dimensions above.

Family **COLUMASTREIDAE** Alloiteau, 1952
Genus **STEPHANAXOPHYLLIA** Alloiteau, 1957

TYPE SPECIES. *Stephanaxophyllia casterasi* Alloiteau, 1957.

Stephanaxophyllia casterasi Alloiteau, 1957
Pl. 3, figs 3, 6

*1957 *Stephanaxophyllia casterasi* Alloiteau: 74, pl. 9, fig. 8.
1982 *Stephanaxophyllia hofergrabenensis* Beauvais, tome I: 128, pl. X, fig. 5.

MATERIAL. AZ 456; AZ 478; AZ 480; AZ 535; AZ 880; AZ 964.

MEASUREMENTS. d (lumen): 2–3.5 mm, in late budding stages up to 6 mm; c–c: 3–5.5 mm; s (monocentric calices): 24–36; size of the colony: 2.5–8 cm in diameter.

DESCRIPTION. Massive or knobby, plocoid colony with calices that are elongated or elliptical in outline. Multiplication is due to extra- and intracalicular budding, resulting in monostomatous to tristomatous conditions. In areas of intensive gemmation the corallites might be polygonal in outline, appearing to be cerioid. Costosepta are compact, nonconfluent, rarely subconfluent, and developed in 3 complete cycles in 6 systems. In general, the beginning of a fourth cycle is present. Septa of the first two cycles slightly alternate in length and thickness. They reach the centre of the calice, where their inner ends may terminate in claviform swellings or dissociate to form paliform structures. Septa of the third cycle may reach nearly three-quarters the length of the oldest ones, occasionally fusing with S₁ or S₂. Septa of the fourth cycle are about half the length of S₃. Columella is papillose or formed by fused segments, resulting in a lamellar appearance. The wall is septothecal and parathecal, in places synapticulothecal, with lacunes. Endotheca consists of numerous thin, vesicular or subtabulate dissepiments. Exotheca is formed by subtabulate dissepiments.

REMARKS. In having synapticulothecal developments and showing intracalicular budding the specimens of the UAE/ Oman more closely correspond to the description of the type species of *Stephanaxophyllia* Alloiteau than to its generic concept given by Alloiteau (1957: 73), in which these characteristics are not mentioned. Moreover, in the description the budding mode is given as ‘generally extracalicular’, whereas the illustration of the type species (Alloiteau, 1957: pl. 9, fig. 8) shows a larger number of dicentric corallites, indicating the strong influence of intracalicular gemmation.

OCCURRENCE. Basal 3 m of Simsim Formation, Jebel Buhays; outcrop at southern tip of Jebel Faiyah ([bed 1] bed 2), NNE of Al Madam; 3 km east of Jebel Rawdah (unit 3), east of Al Madam; Simsim Formation (lowest bed in section), NE corner of Jebel Buhays, 4 km north of Al Madam; Qahlah Formation, *Loftusia* beds, east side of U-shaped Jebel, 10 km NE of Al Ain.

DISTRIBUTION. Santonian of Austria (Gosau Group), Upper Santonian of France.

Genus **COLUMASTREA** d’Orbigny, 1849

TYPE SPECIES. *Astrea striata* Goldfuss, 1826.

Columastrea dubia Alloiteau, 1958 Pl. 3, fig. 5

*1958 (?) *Columastrea dubia* Alloiteau: 186, pl. XXV, fig. 2, pl. XXXIII, fig. 3.

MATERIAL. AZ 47; AZ 507; AZ 512; AZ 554; AZ 898; AZ 916; AZ 925; AZ 927; AZ 936–37; AZ 966; AZ 2534.

MEASUREMENTS. d: 1.2–2.2 mm; dl: (*0.7) 1–1.6 mm; c–c: (*1) 1.5–2.2 mm; s: (*18) 24; size of the colony: 1–9 cm in diameter.

DESCRIPTION. The corallum is massive, knobby, and plocoid, with calices which are rounded or elongated in outline. Costosepta are compact, non- or subconfluent, and are arranged in 3 cycles in 6 systems. Septa of the first cycle reach the centre of the calice, where their inner ends may fuse with the columella or terminate in claviform swellings, which can dissociate to form paliform structures. Second cycle septa can be of the same length, alternating in thickness. Septa

of the third cycle reach about half the length, but are distinctly thinner. Lateral surfaces of septa are covered by delicate spiniform granules. Columella is styliiform. The wall is septothecal. Endotheca consists of thin, vesicular dissepiments.

OCCURRENCE. SE corner of Jebel Huwayyah (bed 8, 9), east of Al Ain; *Loftusia* Beds, Qahlah Formation, SE corner of Jebel Huwayyah, east of Al Ain; ; east face of northern hill forming Jebel Buhays, 4 km north of Al Madam; outcrop at southern tip of Jebel Faiyah, 6 km NNE of Al Madam; Qahlah Formation, east side of U-shaped Jebel, 10 km NE of Al Ain.

DISTRIBUTION. Upper Campanian of Madagascar.

Family **PLACOCOENIIDAE** Alloiteau, 1952

Genus **PARAPLACOCOENIA** Beauvais, 1982

TYPE SPECIES. *Placocoenia orbignyana* Reuss, 1854.

Paraplacocoenia orbignyana (Reuss, 1854) Pl. 4, fig. 1

- ?1850 *Phyllocoenia marticensis* d'Orbigny, tome II: 204.
- v*1854 *Placocoenia orbignyana* Reuss: 99, pl. 9, figs. 1, 2.
- 1857 ?*Cyphastraea orbignyana* (Reuss); Milne Edwards & Haime, tome II: 277.
- 1899 *Phyllocoenia excelsa* Fromentel; Söhle: pl. 10, fig. 1.
- v1903a *Placocoenia orbignyana* Reuss; Felix: 296, fig. 48.
- 1914 *Placocoenia orbignyana* Reuss; Felix, pars 7: 155.
- ?1914 *Phyllocoenia marticensis* d'Orbigny; Felix, pars 7: 158.
- ?1937 *Placocoenia orbignyana* Reuss; Bataller: 105.
- v1982 *Paraplacocoenia orbignyana* (Reuss); Beauvais, tome I: 114, pl. 9, figs. 1, 2 (older synonyms cited therein).
- v1999 *Paraplacocoenia orbignyana* (Reuss); Baron-Szabo: pl. 4, fig. 4, pl. 7, figs. 1–2, text-fig. 2.

MATERIAL. AZ 209–10; AZ 513; AZ 523; AZ 545; AZ 549–51; AZ 563; AZ 582; AZ 884; AZ 946–47; AZ 962–63.

MEASUREMENTS. d: 3–5.5 (*6.5) mm; dl: 2–3.5 (*4) mm; c–c: 2.5–6.5 (*7) mm; s: 24 + s3; size of the colony: 6–14 cm in diameter.

DESCRIPTION. Massive and plocoid corallum, with circular or slightly elliptical calices. Increase is by extracalicular budding. Costosepta are compact, nonconfluent, occasionally subconfluent, and arranged in 3 complete cycles in 6 regular systems. In some calices the beginning of a fourth cycle is present. Septa of the first cycle extend to the centre of the corallite. Their inner ends may be cuneiform, irregularly thickened, or may produce trabecular prolongations, which fuse with the columella. Second cycle septa are almost of the same length, but alternate in thickness. Septa of the third cycle regularly alternate in length and thickness. Youngest septa are distinctly thinner and shorter than the ones of the preceding cycle. Septal flanks are covered by rounded or spiniform granules. Intercorallite areas are crossed by costae, rarely dissociating into a reticulated coenenchyme. Columella is lamellar, short, thin, or rudimentary. Wall is septothecal, septoparathecal, and rarely ?synapti-

culothecal. Endotheca is formed by thin, vesicular and tabulate dissepiments. Exotheca consists of vesicular or cellular dissepiments.

REMARKS. Beauvais (1982) lists *Paraplacocoenia orbignyana* (Reuss) as a junior synonym of *Phyllocoenia marticensis*, but gives the first priority over the latter. Because the author has not seen the type of *Phyllocoenia marticensis*, *Paraplacocoenia orbignyana* (Reuss) is tentatively regarded as a primary species (previously discussed in Baron-Szabo, 1999). However, the Oman specimens very closely agree with the type material of *Paraplacocoenia orbignyana* (Reuss).

OCCURRENCE. *Loftusia* Beds, Qahlah Formation, east side of U-shaped Jebel, 10 NE of Al Ain; outcrop on east face, ca. 3 km north of the southern tip of Jebel Faiyah, NNE of Al Madam; *Loftusia* Beds, Qahlah Formation, SE corner of Jebel Huwayyah (beds 10/11), east of Al Ain; scree slope at SW corner of Jebel Buhays, 4 km north of Al Madam; outcrop at southern tip of Jebel Faiyah, 6 km NNE of Al Madam; NE slope of valley at Qarn Murrah, 15 km north of Al Madam; NE slope of valley at Qarn Murrah, 8 km west of northern tip of Jebel Faiyah, 15 km north of Al Madam.

DISTRIBUTION. Upper Cretaceous of southern France (Provence), Santonian of northeastern Spain (Catalonia), Santonian-Campanian of Austria (Gosau Group).

Genus **ASTROGYRA** Felix, 1900

TYPE SPECIES. *Gyrosmlia edwardsi* Reuss, 1854.

Astrogyra edwardsi (Reuss, 1854)

Pl. 5, fig. 1, Pl. 6, fig. 4

- v*1854 *Gyrosmlia edwardsi* Reuss: 92, pl. IV, figs 1–3.
- 1857 *Thecosmlia ? edwardsi* (Reuss); Milne Edwards, tome II: 362.
- 1900 *Astrogyra edwardsi* (Reuss); Felix: 2.
- non 1930 *Astrogyra edwardsi* (Reuss); Oppenheim: 308, pl. XXXII, figs 5, 5a.
- 1937 *Astrogyra edwardsi* (Reuss); Bataller: 120, text-fig. 121.
- 1956 *Astrogyra edwardsi* (Reuss); Bendukidze: 91, pl. I, fig. 5, pl. VII, figs 8, 8a.
- 1982 *Astrogyra edwardsi* (Reuss); Beauvais, tome I: 78, pl. V, fig. 2 (older synonyms are cited therein).

MATERIAL. AZ 421; AZ 423–26; AZ 428; AZ 463; AZ 474–75; AZ 577; AZ 647; AZ 665; AZ 97–75.

MEASUREMENTS. d (series including peritheca): (*12) 18–25 (*30) mm; d (ambulacrum): 1–5 mm; s/mm: 10–18/10; size of the colony: 12–15 cm in diameter.

DESCRIPTION. The corallum is massive and meandroid, with corallites that are arranged in parallel, or wavy series. Series are united by perithecal walls, which are marked by ambulacrae. Costosepta are compact, non-confluent, thin, straight, and developed

PLATE 4

Micrographs of plocoid (1, 4), cerioid (2, 5) and branching phaceloid (3) coral colonies in transverse thin-sections.

Fig. 1 *Paraplacocoenia orbignyana* (Reuss, 1854); AZ 513.

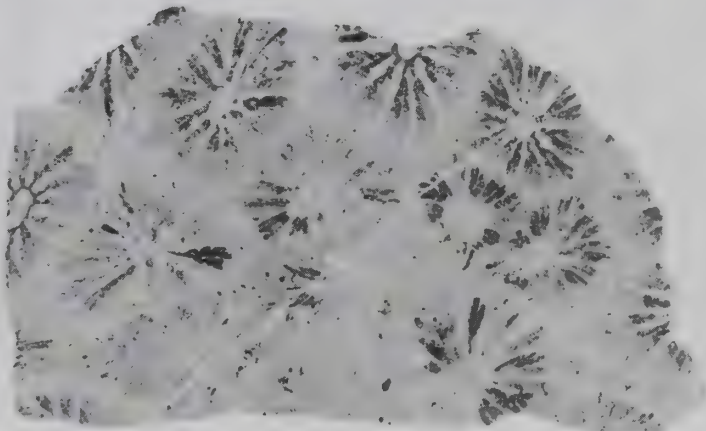
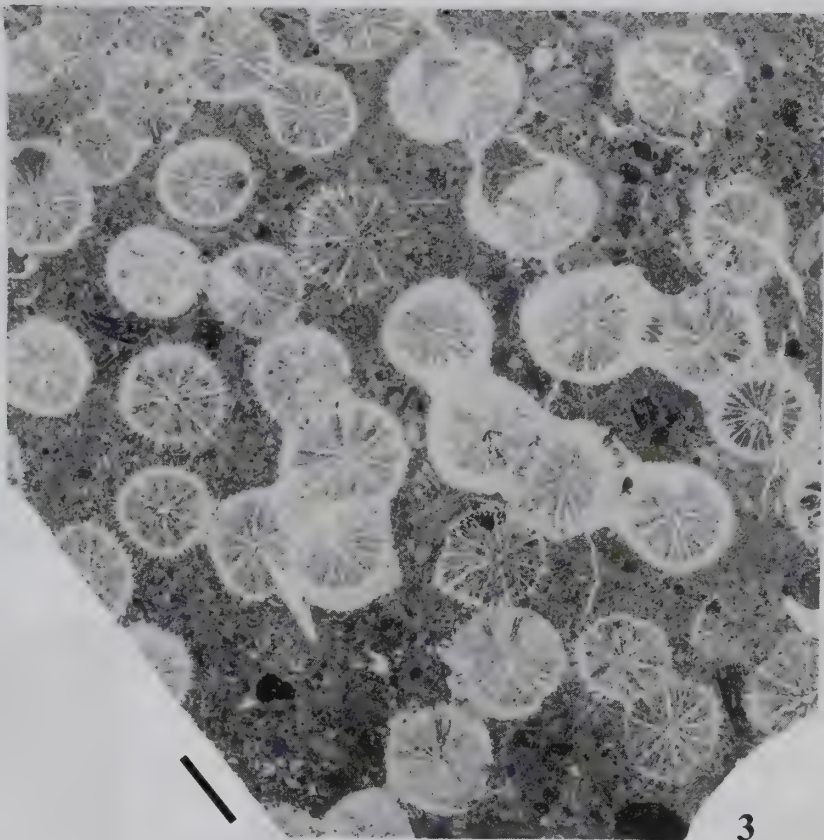
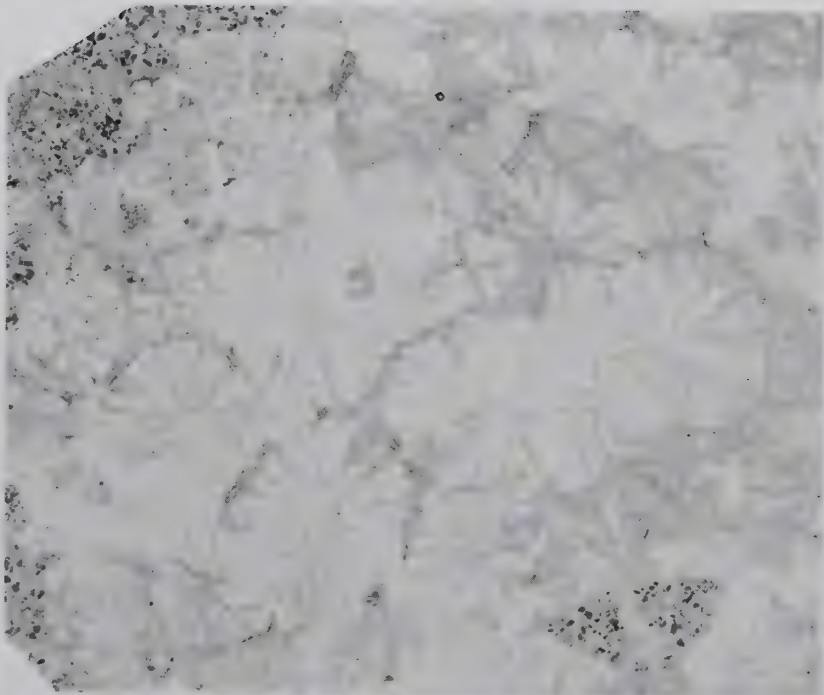
Fig. 2 *Glenarea cretacea* Poeta, 1887; AZ 429.

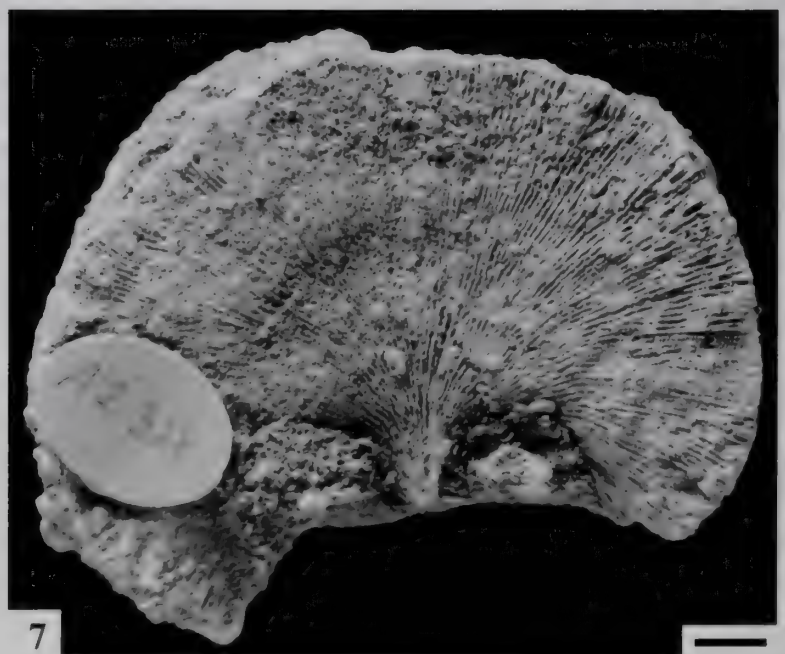
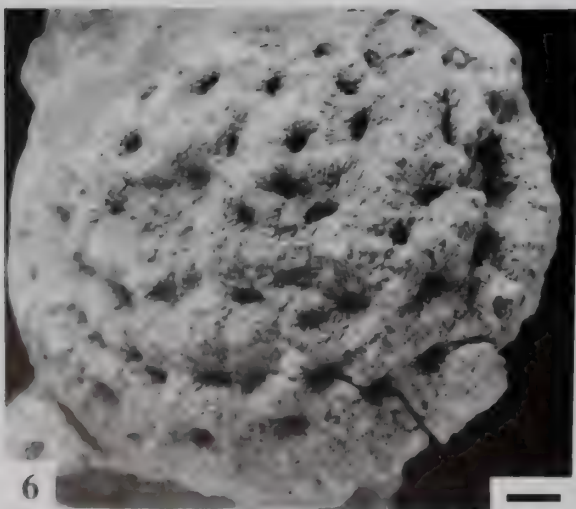
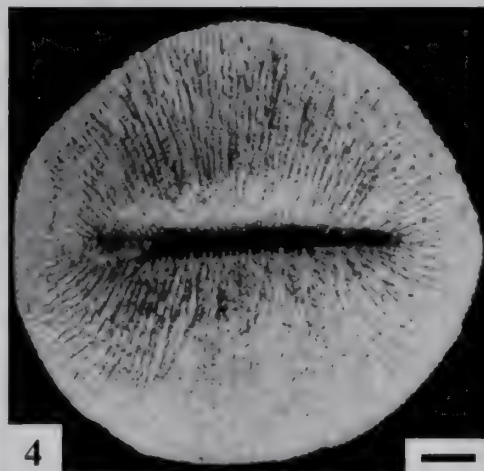
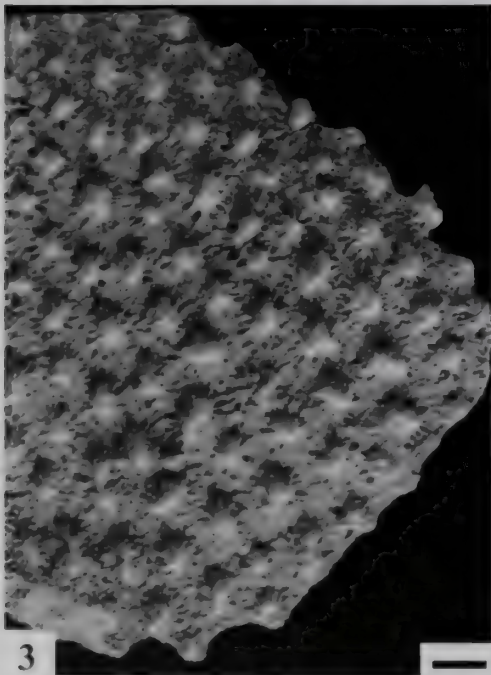
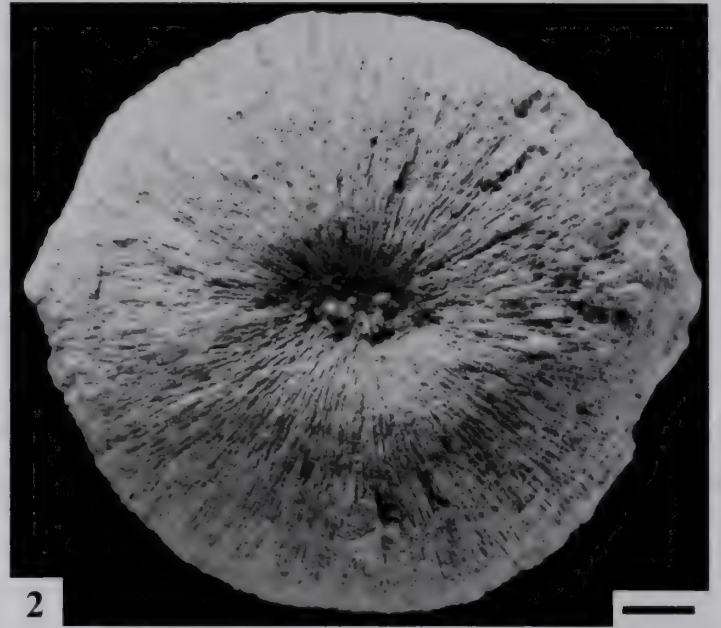
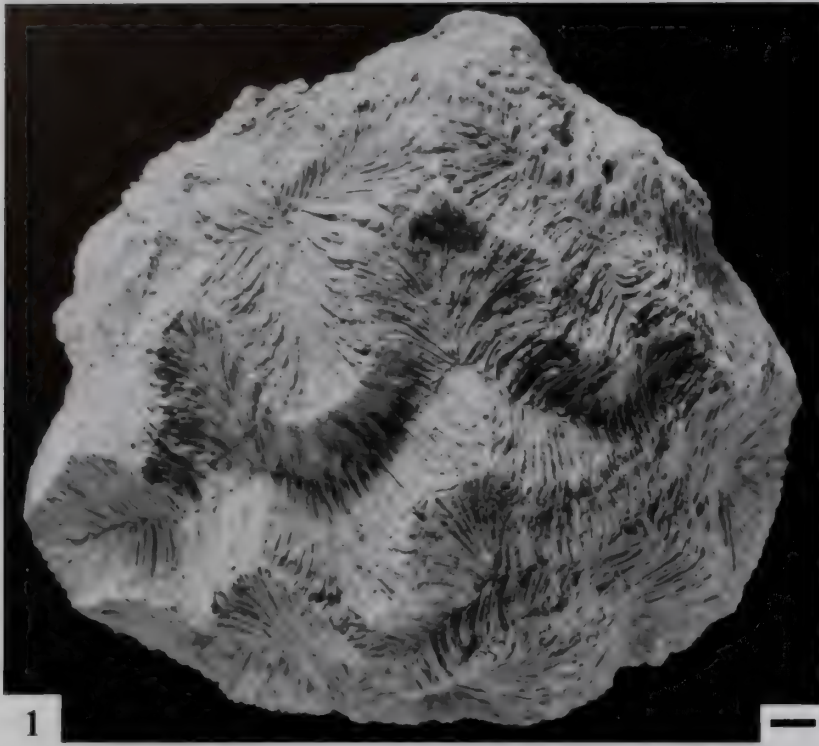
Fig. 3 *Cladophyllia stewartae* Wells, 1944; AZ 575.

Fig. 4 *Agathelia asperella* Reuss, 1854; AZ 895.

Fig. 5 *Diplocoenia* cf. *parvistella* Alloiteau, 1958; AZ 457.

Scale bar = 3 mm.





in 3 orders. In places the beginning of a fourth order is present. Septal flanks are finely granulated. Septa of the first two orders are of the same length, but differ in thickness. Their inner ends are rhopaloid or claviform. Trabecular prolongations of their inner ends may extend to, and fuse with, the columella. Septa of the third order reach about half the length of S1 and S2. Columella is lamellar, very thin and discontinuous. Endotheca consists of numerous vesicular or subtabulate dissepiments.

REMARKS. According to Beauvais (1982, tome I: 80) *Astrogyra edwardsi* (Reuss) in Oppenheim represents a younger synonym of *Astrogyra orbignyi* (Fromentel).

OCCURRENCE. *Loftusia* Levels, Beds 3–8, SW of Jebel Huwayyah; outcrop forming slope on north side of valley (beds 13, 15, 19), ca. 2 km east of Jebel Rawdah, east of Al Madam.

DISTRIBUTION. Upper Cretaceous of Romania, Senonian of Georgia (in Caucasia), Santonian of Austria (Gosau Group), Upper Santonian of northern Spain (Catalonia).

Family **PLACOSMILIIDAE** Alloiteau, 1952

Genus **PLACOSMILIA** Milne Edwards & Haime, 1848

TYPE SPECIES. *Turbinolia cymbula* Michelin, 1846.

Placosmilia sinuosa (Reuss, 1854) Pl. 6, fig. 5

*1854 *Euphyllia sinuosa* Reuss: 92, pl. XVI, fig. 3.

1857 *Thecosmilia* ? *sinuosa* (Reuss); Milne Edwards, tome II: 360.

1900 *Lasmogyra irregularis* Felix: 3.

1982 *Placosmilia sinuosa* (Reuss); Beauvais, tome I: 62, pl. III, fig. 3 (older synonyms cited therein).

MATERIAL. AZ 46; AZ 59; AZ 940.

MEASUREMENTS. d (max): 80–125 mm; d (min): 20–40 mm; s/mm: 15–19/10; h: 4–9 cm.

DESCRIPTION. Flabelliform corallum, very elongate in outline. Costosepta are compact and straight, becoming wavy toward the axial region. Three size orders of septa irregularly alternate in length and thickness. In some parts the beginning of a fourth order is present. Septa of the first two orders reach the centre of the corallum. Their inner ends terminate in claviform or rhopaloid thickenings, giving off trabecular prolongations which may meet with both neighbouring septa or with the columella. Septal flanks are covered by delicate rounded granules. The columella is very thin, lamellar and discontinuous. Wall is parathecal-epicostate. In places an epithecal wall can be observed. Endotheca is made of vesicular dissepiments. Microstructure is poorly preserved. Occasionally, mini- to medium-sized trabeculae can be seen.

REMARKS. In the description of the type material of *Placosmilia sinuosa* (Reuss), Beauvais (1982, tome I: 62 and table 1) gives the minimum diameter ranging from 29.5 to 34.5 mm and the density of

septa of 10 in 10 mm. In contrast, the photograph of the type presented by Beauvais (1982, tome IV, pl. III, fig. 3) reveals the dimensions 19 up to around 40 mm for the minimum diameter and the density of septa of around 20 in 10 mm, thus completely agreeing with the original description by Reuss (1854: 92). Assuming that Beauvais' data represent printing errors, it can be stated that the specimens at hand very closely correspond with the Austrian material.

OCCURRENCE. Main coral bed, *Loftusia* levels (beds 7, 10/11), SW and SE corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Upper Santonian of Austria (Gosau Group) and southern France (Corbières).

Family **ISASTREIDAE** Alloiteau, 1952

Genus **DIPLOCOENIA** Fromentel, 1857

TYPE SPECIES. *Diplocoenia mirabilis* Fromentel, 1857.

Diplocoenia cf. parvistella Alloiteau, 1958 Pl. 4, fig. 5

*1958 *Diplocoenia parvistella* Alloiteau: 159, pl. XI, fig. 2.

MATERIAL. AZ 457.

MEASUREMENTS. d (max): 2–4 (*5) mm; d (min): 2–3.5 mm; c–c: 2.5–4.5 mm; s: 28–48; size of the colony: about 5 cm in diameter.

DESCRIPTION. Massive cerioid or subplocoid colony with corallites that are polygonal, subcircular, or elliptical in outline. Gemmation is due to extra- and intracalicular budding. Calices are directly united by their walls (regions with cerioid development) or are separated by small scaled intercorallite areas (resulting in a subplocoid arrangement). Costosepta are compact, straight, and developed in 3 to 4 cycles in 6 systems. Septa of the first two cycles extend the centre of the corallite where their inner ends may terminate in irregular thickenings, sometimes fusing with the columella. Septa of the third cycle are distinctly thinner, reaching about three-quarters the length of the oldest ones. Septa of the fourth cycles are very thin and short. Lateral surfaces of the septa are covered by thick rounded or delicate spiny granules. The columella is well-developed styliform to substyliform, or irregularly trabecular. Wall is parathecal, in places ?septothecal.

REMARKS. The calicular diameter in specimen of the UAE/ Oman is slightly larger than in *Diplocoenia parvistella* Alloiteau, but otherwise agrees well with it.

OCCURRENCE. Basal 3 m of Simsim Formation, east face of most northern hill forming Jebel Buhays, 4 km north of Al Madam.

DISTRIBUTION. Coniacian of Madagascar.

Family **DERMOSMILIIDAE** Koby, 1889

Genus **CALAMOPHYLLIOPSIS** Alloiteau, 1952

TYPE SPECIES. *Calamophyllia flabellata* Fromentel, 1861.

PLATE 5

Micrographs of meandroid (1), flabello-meandroid (5, 7), (hydno-phoro-) meandroid (3), thamnasterioid (6), and discoid (2, 4) coralla in upper surface view.

Fig. 1 *Astrogyra edwardsi* (Reuss, 1854); AZ 975.

Figs 2, 4 *Cunolites* sp.; 2, AZ 400; 4, AZ 865.

Fig. 3 *Monticulastraea insignis* Duncan, 1880; AZ 656.

Figs 5, 7 *Diploctenium lunatum* (Bruguère, 1792); 5, AZ 2526; 7, AZ 328.

Fig. 6 *Aspidastraea orientalis* Kühn, 1933; AZ 189.

Scale bar = 3 mm.

***Calamophylliopsis simonyi* (Reuss, 1854) Pl. 9, fig. 4**

- v*1854 *Cladocora simonyi* Reuss: 112, pl. XII, figs 5–7.
 1857 *Cladocora ? simonyi* Reuss; Milne Edwards, tome II: 598.
 1861 *Cladocora ? simonyi* Reuss; Fromentel: 150.
 v1903a *Cladocora simonyi* Reuss; Felix: 266, text-fig. 33.
 1914 *Cladocora simonyi* Reuss; Felix, pars 7: 171.
 1930 *Cladocora simonyi* Reuss; Oppenheim: 360.
 non 1976 *Procladocora simonyi* (Reuss); Turnšek, in Turnšek & Buser: 56, 79, pl. 12, figs 1, 2.
 non 1978 *Procladocora simonyi* (Reuss); Turnšek, in Turnšek & Polšák: 151, 171, pl. 7, figs 1–7.
 1982 *Calamophylliopsis simonyi* (Reuss); Beauvais, tome II: 233, fig. 2.

MATERIAL. AZ 580.

MEASUREMENTS. d (adult): 5–8 mm; d (juvenile): 3–4; s: 36–52; size of the colony: 13 cm in diameter.

DESCRIPTION. The corallum is in the form of a phaceloid colony with circular or slightly elliptical corallites. Costosepta are compact with rare perforations, thin, straight, and are generally arranged in 4 complete cycles in 6 systems. Septa of the first cycle reach the centre of the corallite, where trabecular prolongations of their inner ends may join or fuse with the columella. Second and third cycle septa can be nearly equal in length and thickness. Youngest septa are distinctly thinner and shorter. Lateral surfaces of septa are covered with delicate spiniform and rounded granules. Occasionally, synapticalae can be seen. The columella is parietal, well-developed. Wall is septoparathecal. Endotheca consists of thin subtabulate dissepiments. An epithecal wall is always present. Microstructure is poorly preserved, but in places simple minitraculae are present (wall and septa), forming wavy axial lines.

OCCURRENCE. Main coral bed (*Loftusia* levels, bed 7), SW corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Santonian of Austria (Gosau Group).

Suborder **STYLININA** Alloiteau, 1952
 Family **AGATHELIIDAE** L. & M. Beauvais, 1975
 Genus **AGATHELIA** Reuss, 1854

TYPE SPECIES. *Agathelia asperella* Reuss, 1854.

***Agathelia asperella* Reuss, 1854 Pl. 4, fig. 4**

- v*1854 *Agathelia asperella* Reuss: 82, pl. IX, figs 10–12.
 v1903a *Agathelia asperella* Reuss; Felix: 262, text-figs 30, 32.
 1926 *Agathelia urgonica* Dietrich: 75, pl. V, fig. 1, pl. VIII, fig. 2.
 ?1937 *Agathelia asperella* Reuss; Bataller: 141.
 v1975 *Agathelia asperella* Reuss; L. & M. Beauvais: 567, text-fig. 1, fig. 2, text-fig. 2, figs 1, 2.

- v1982 *Agathelia asperella* Reuss; Beauvais, tome I: 44, pl. LXI, fig. 7, pl. LXII, figs 1, 2.
 1987 *Agathelia asperella* Reuss; Kuzmicheva: 81, pl. II, fig. 1.
 v1989 *Agathelia asperella* Reuss; Höfling: 55.
 v1992 *Agathelia asperella* Reuss; Eliášová: 405, pl. VI, fig. 1.
 1994 *Agathelia asperella* Reuss; Liao & Xia: 69, pl. V, text-figs 43a–c.
 v1997 *Agathelia asperella* Reuss; Baron-Szabo: 35, pl. 1, figs 1, 3, 5 (older synonyms cited therein).
 1997 *Agathelia asperella* Reuss; Eliášová: 246 ff.

MATERIAL. AZ 434; AZ 520; AZ 895; AZ 899; AZ 950.

MEASUREMENTS. d: 3.5–6 mm; d (juvenile): 1.5–2.5 mm; dl: 2.5–4.5 mm; c–c: (*2.5) 3–5.5 mm; s: 24–48 +s5; s (juvenile): 16–22; size of the colony: up to 13 cm in diameter.

DESCRIPTION. Massive and plocoid colony with calices that are subcircular or elliptical in outline. Multiplication is due to extracalicular budding. Costosepta are compact, thin, straight, and arranged in 3 to 4 cycles in 6 systems. In some calices the beginning of a fifth cycle is present. Septa of the first two cycles are nearly equal in length and thickness, slightly alternating. They extend to the centre of the corallite, where their inner ends may terminate in claviform thickenings. Septa of the third and fourth cycle are distinctly thinner and reach about half the length of the ones of the preceding cycle. Their inner ends are cuneiform or stretch out forming auricularae. Lateral surfaces of septa are covered with spiniform and rounded granules, sometimes appearing as vertical subcarinae. The columella is lamellar, discontinuous in some calices. The wall is septothecal, in places parathecal. Endothecal dissepiments are thin and slightly arched. Exotheca consists of large vesicular dissepiments. Septal microstructure corresponds to the stylinid type illustrated in Roniewicz (1996), with medium to thick main trabeculae giving off secondary ones. The wall is formed by densely packed polyaxial trabeculae, with predominantly thick centres of calcification.

OCCURRENCE. East face of most northern hill forming Jebel Buhays, 4 km north of Al Madam; outcrop forming east face, ca. 3 km north of southern tip of Jebel Faiyah, NNE of Al Madam; coral/stromatoporoid level (bed 4), ca. 3 km east of Jebel Rawdah, east of Al Madam; *Loftusia* beds (bed 5), SE corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Hauterivian of the Crimea, Barremian-Aptian of Tanzania, Albian-Cenomanian of Tibet, Upper Cenomanian-Lower Turonian of the Czech Republic, ?Upper Turonian-Lower Coniacian and Santonian-Campanian of Austria (Gosau Group), Santonian of Armenia, Santonian-Campanian of Slovakia, ?Maastrichtian of northern Spain.

Family **CLADOPHYLLIIDAE** Morycowa & Roniewicz, 1990
 Genus **CLADOPHYLLIA** Milne Edwards & Haime, 1851

TYPE SPECIES. *Lithodendron dichotomum* Goldfuss, 1826.

PLATE 6

Micrographs of solitary (1, 2), meandroid (4), flabello-meandroid (5), branching phaceloid (3) coralla in transverse thin-sections and upper surface view.

Fig. 1 *Aulosmilia aspera* (Sowerby, 1831); AZ 56.

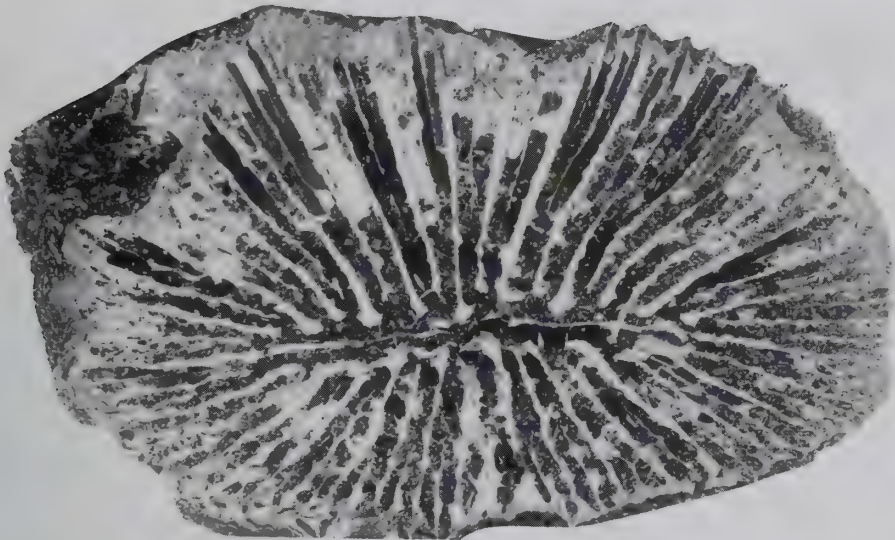
Fig. 2 *Phragmosmilia lineata* (Goldfuss, 1826); AZ 60.

Fig. 3 *Cladophyllia stewartae* Wells, 1944; AZ 643.

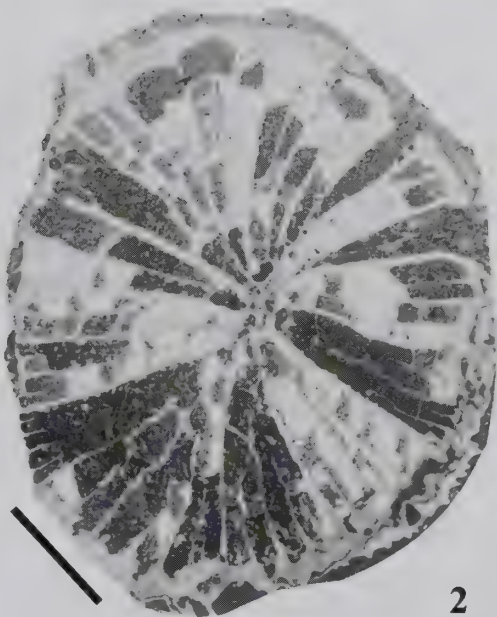
Fig. 4 *Astogyra edwardsi* (Reuss, 1854); AZ 421.

Fig. 5 *Placosmilia sinuosa* (Reuss, 1854); AZ 59.

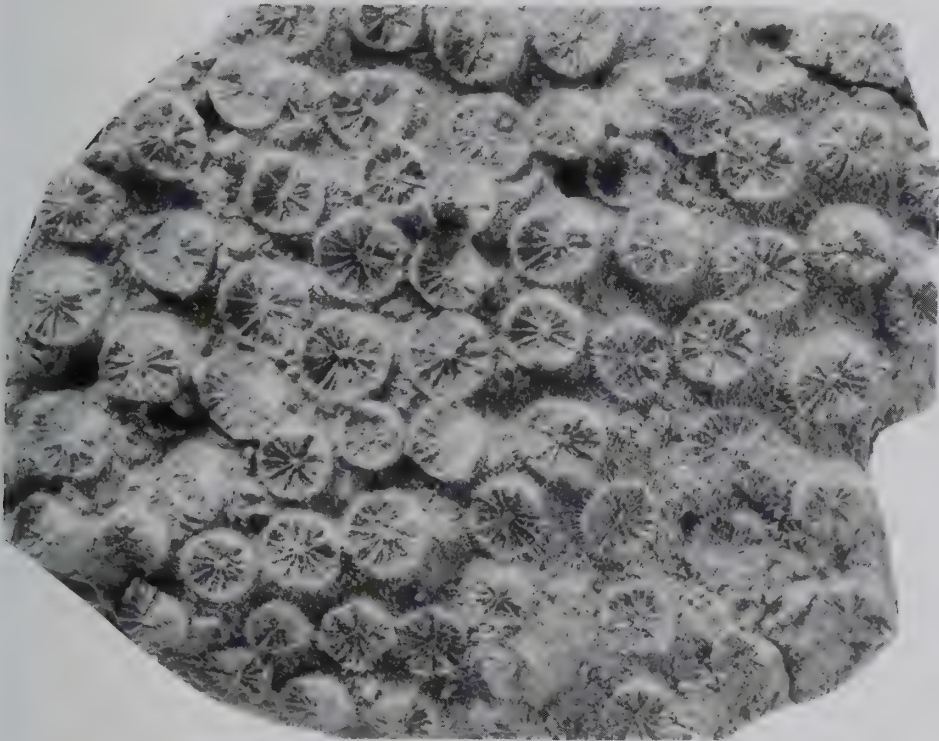
Scale bar = 3 mm.



1



2



3



4



5



Fig. 6 Stages of corallite division in *Cladophyllia minor* Beauvais, 1975, upon which the model of 'septal division' was established by Morycowa & Roniewicz (1990): 1 = initial stage characterized by fusion of septa; 2 = advanced stage with new septa on the wall surface developed; 3 = late stage with median wall line marked and a constriction developing between two corallites. Scale bar = 2 mm.

***Cladophyllia stewartae* Wells, 1944 Pl. 4, fig. 3, Pl. 6, fig. 3**

*1944 *Cladophyllia stewartae* Wells: 442, pl. 74, figs 2, 3.

1990 *Cladophyllia stewartae* Wells; Morycowa & Roniewicz: 168.

MATERIAL. AZ 375; AZ 575; AZ 579; AZ 643; AZ 973.

MEASUREMENTS. d: (*2.5) 3–4 mm; s: 24 (*+s₄); size of the colony: up to 17 cm in diameter.

DESCRIPTION. The corallum is phaceloid, with corallites that are circular or slightly elongated in outline and having a diameter of 3 mm on average. Budding is due to 'septal division' (*sensu* Morycowa & Roniewicz, 1990; see Fig. 6). Costosepta are compact, straight, with lateral surfaces that are covered by sharply pointed or rounded granules, and are arranged in 3 complete cycles in 6 systems. Frequently, the beginning of a fourth cycle is present. Septa of the first two cycles reach the centre of the calice, where their inner ends may fuse. A trabecular, styliiform, or sublamellar columella can be free or joined with oldest septa. Septa of the third cycle are distinctly thinner, reaching about three-quarters the length of the oldest ones. Youngest septa are very small and thorn-like. Anastomosis can be observed frequently. The wall is septothecal. Endotheca is made of tabulate dissepiments in the axial part of the corallite. In the peripheral region of the calice large vesicular dissepiments occur. Septal microstructure consists of simple minitraculae, forming dark axial lines.

REMARKS. In having a calicular diameter of 3 mm on average with a septal development of 3 cycles in 6 systems, and the first two septal cycles being nearly equal, the UAE/ Oman specimens closely agree with *Cladophyllia stewartae* Wells.

OCCURRENCE. *Loftusia* level, main coral bed (bed 7), SW corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Upper Aptian-Lower Albian of Venezuela.

Suborder **MEANDRIINA** Alloiteau, 1952
Family **DENDROGYRIIDAE** Alloiteau, 1952
Genus **DIPLOCTENIUM** Goldfuss, 1826

TYPE SPECIES. *Diploctenium cordatum* Goldfuss, 1826.

***Diploctenium lunatum* (Bruguière, 1792) Pl. 5, figs 5, 7**

*1792 *Madrepora lunata* Bruguière, tome I: 461, pl. 24, figs. 5–6.

1826 *Diploctenium cordatum*: Goldfuss (pars): 105, pl. XXXVII, fig. 16.

1849 *Diploctenium lunatum* (Bruguière); Milne Edwards & Haime, 3e sér., tome X: 248.

1851 *Diploctenium lunatum* (Bruguière); Milne Edwards & Haime: 50.

1863 *Diploctenium lunatum* (Bruguière); Fromentel: 248, pl. XIV, fig. 3.

1892 *Diploctenium lunatum* (Bruguière); Mallada: 160.

v1903a *Diploctenium lunatum* (Bruguière); Felix: 347, fig. 65.

1930 *Diploctenium angusterimatum* (Bruguière); Oppenheim: 533, pl. XLI, figs 10, 10a.

1937 *Diploctenium lunatum* (Bruguière); Bataller: 243.

1941 *Diploctenium lunatum* (Bruguière); Alloiteau: 51, pl. XXI, figs 1–3.

1952b *Diploctenium lunatum* (Bruguière); Alloiteau: 542, fig. 4.

1965 *Diploctenium lunatum* (Bruguière); Bendukidze: 20–24, pl. 2–4.

1982 *Diploctenium lunatum* (Bruguière); Beauvais, tome I: 164–167 (older synonyms cited therein).

v1998 *Diploctenium lunatum* (Bruguière); Baron-Szabo: 143, pl. 7, fig. 3.

?v1999 *Diploctenium* sp.; Baron-Szabo: pl. 6, figs 1–2.

MEASUREMENTS. Height of corallum from stem to upper surface (st): 17–28 mm; height of corallum from the extremities to upper surface (e): 12–46 mm; d (min): 3–9 mm; d (max): 20–42 mm; s/ mm: 12–15/5.

Measurements (in mm) of the skeletal elements:

	st	e	d (max)	d (min)
AZ 503	28	46	40	4–5
AZ 739	25	26	39	7–9
AZ 328	24	30	35	5–7
AZ 204	23	?26	42	4.5–5.5
AZ 318	23	25	32	6–8
AZ 317	22	25	32	6–7
AZ 2526	21	24	26	3–4
AZ 738	20	23	23	5–7
AZ 316	20	12	?	5–6
AZ 437	19	16	25	3.5–6
AZ 633	18	20	26	3–5.5
AZ 319	?18	14	20	4–7
AZ 493	17	37	35	3.5–6.5

DESCRIPTION. The corallum is flabelliform, elongate, elliptical, or arched so strongly that the extremities of its longer axis may descend below the stem. Costosepta are compact, straight, and developed in

two orders with an incomplete third order. Septa of the first order extend to, and may fuse with, the columella. Septa of the second order are nearly equal in thickness, but slightly alternating in length. S3 are much thinner and may reach about one to three-quarters the length of the oldest ones. Septal flanks are covered with delicate spiniform granules. Inner ends of septa can be slightly thickened. The columella is thin, lamellar and discontinuous. The endotheca consists of thin dissepiments. The wall is septothecal.

REMARKS. Bendukidze (1956, 1965) studied the stages of ontogeny of specimens of *Diploctenium lunatum* (Bruguière). She concluded that skeletal elements and their dimensions in this species are directly dependent upon environment. Moreover, within the same specimen each stage of ontogeny closely corresponds to a different species of *Diploctenium*. These results completely disagree with the generic concept proposed by Alloiteau (1952a, b) (see also discussion in Beauvais 1982, tome I: 164 ff.). It seems necessary to investigate more specimens of different species of this genus to evaluate the pertinent taxonomical criteria. Specimens at hand closely agree with the descriptions and illustrations of *Diploctenium lunatum* by Bendukidze (1956, 1965) (previously discussed in Baron-Szabo, 1998).

Details closely agreeing with the septal development in the UAE/Oman specimens have been previously well illustrated (Baron-Szabo, 1999: pl. 6, fig. 1).

OCCURRENCE. *Trigonia/Pachymyra* Bed, east of Jebel Rawdah, east of Al Madam; east face of most northern hill forming Jebel Buhays, 4 km north of Al Madam (loose from beds 4–11); Simsima Formation, 3 km east of Jebel Rawdah, east of Al Madam; above *Zuffardia* level (bed 13), north side of valley, ca. 2 km east of Jebel Rawdah, east of Al Madam; north side of valley, ca. 3 km east of Jebel Rawdah, east of Al Madam.

DISTRIBUTION. Upper Cretaceous of Romania, Santonian-Campanian of Austria (Gosau Group), Turonian and Santonian-Maastrichtian of northern Spain (Catalonia), Upper Santonian of southern France (Provence and Corbières).

MATERIAL. See list in Measurements above.

Family **MEANDRIIDAE** Alloiteau, 1952

Subfamily **MEANDRIINAE** Vaughan & Wells, 1943

Genus **AULOSMILIA** Alloiteau, 1952

TYPE SPECIES. *Trochosmilia archiaci* Fromentel, 1867.

Aulosmilia aspera (Sowerby, 1832) Pl. 6, fig. 1

*1832 *Turbinolia aspera* Sowerby, in Sedgewick & Murchison: 417, pl. 37, fig. 1.

1857 *Montlivaultia rudis* Milne Edwards, vol. II: 314 (pars).

1863 *Placosmilia arcuata* Milne Edwards & Haime; Fromentel: 219, pl. 19, figs 1–4.

1914 *Trochosmilia chondrophora* Felix; Felix, pars 7: 213 (pars).

1974 *Aulosmilia aspera* (Sowerby); L. & M. Beauvais: 485.

1978 *Aulosmilia aspera* (Sowerby); Turnšek: 72, 104, pl. 3, figs. 1–4.

1982 *Aulosmilia aspera* (Sowerby); Beauvais, tome I: 218, pl. 18, fig. 6, pl. 19, fig. 2.

1987 *Aulosmilia aspera* (Sowerby); Kuzmicheva: 61.

v1998 *Aulosmilia aspera* (Sowerby); Baron-Szabo: 139, pl. 3, fig. 5, text-fig. 4.

v1999 *Aulosmilia aspera* (Sowerby); Baron-Szabo: pl. 6, fig. 5.

MATERIAL. AZ 50; AZ 55–56; AZ 73; AZ 795.

MEASUREMENTS. d (max) (D): 20–37 mm; d (min) (d): 13–27 mm; s: 120–140; h: 20–55 mm; d/D: 0.70–0.80.

DESCRIPTION. The corallum is simple, turbinate or ceratoid, elongated in outline. Costosepta are compact, thin, long, and arranged in 4 size orders, regularly alternating in thickness. Twenty to 24 septa reach the centre of the corallite, where they become slightly curved or flexuous. Their inner ends are cuneiform or terminate into claviform thickenings. Septa of the second order, being 20–24 in number, are distinctly thinner, but can be nearly of the same length. The third order consists of about 20 septa, which are very thin, reaching about half to three-quarters the length of septa of the preceding order. Septa of following orders are very short and thin. Columella is lamellar, thin and wavy. Endotheca consists of vesicular dissepiments, which mainly occur in the peripheral region of the corallum. The wall is septothecal. In places an epithecal wall is present.

REMARKS. The specimens from UAE/Oman very closely agree with the Campanian material of northern Spain (Baron-Szabo, 1998: 139, text-fig. 4). In coralla showing stages of rejuvenation the number of septa forming an order may be slightly larger (around 30), and the ratio d/D may be slightly smaller than the above given (0.62).

OCCURRENCE. *Loftusia* Level, Main Coral Bed (beds 3–8), SW corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. (?Upper Turonian-) Lower Coniacian-Santonian of Austria (Gosau Group), Middle Coniacian and Upper Santonian of southern France (Corbières, Provence), Santonian-Campanian of northwestern Croatia and Slovenia, Campanian of northern Spain.

Genus **GLENAREA** Pöcta, 1887

TYPE SPECIES. *Glenarea cretacea* Pöcta, 1887.

Glenarea cretacea Pöcta, 1887 Pl. 4, fig. 2

*1887 *Glenarea cretacea* Pöcta: 25, text-figs 9, 10.

non 1974 *Glenarea cretacea* Pöcta; Turnšek, in Turnšek & Buser: 20, 100, pl. 10, fig. 2.

v1991 *Glenarea cretacea* Pöcta; Eliášová: 99, pl. I, figs 1a, b.

1997b *Glenarea cretacea* Pöcta; Eliášová: 258.

MATERIAL. AZ 285; AZ 429–30; AZ 543.

MEASUREMENTS. d (max): 2.5–7 mm; d (min): 1.5–4.5; s: 12–24, s/mm: 3–4/2; size of the colony: 6–7 cm in diameter.

DESCRIPTION. The corallum is massive, hemispherical and cerioid, with corallites directly united by their walls and are polygonal or slightly rounded in outline. Gemmation is due to intracalicular budding, which resembles the ‘septal division’ in its early stage (*sensu* Morycowa & Roniewicz, 1990; see Fig. 6). Costosepta are compact, straight, thin, nonconfluent, nearly equal in thickness, and are radially arranged in two to three cycles in 6 systems. In corallites which are influenced by gemmation a bilateral or irregular septal development is present. Four to 12 septa reach the axial region, where their inner ends may extend to, and fuse with, the columella or neighbouring septa. First and second cycle septa can be nearly equal in length. Remaining septa regularly alternate in length. Anastomosis is seen frequently. Septal flanks are finely granulated. The columella is short, lamellar. Wall is septothecal and septoparathecal. Endotheca consists of thin vesicular dissepiments. Microstructure is poorly preserved, but in some septa simple minitraculae, forming wavy mid-septal lines are observed.

OCCURRENCE. Outcrop on east face, ca. 3 km north of the southern tip of Jebel Faiyah (bed 10), NNE of Al Madam; Coral bed (*L. hemipneustes* bed), top bed 13, outcrop forming slope and cliff on north side, about 2 km east of Jebel Rawdah, east of Al Madam.

DISTRIBUTION. Upper Cenomanian-Lower Turonian of the Czech Republic.

Genus **PHRAGMOSMILIA** Alloiteau, 1952

TYPE SPECIES. *Trochosmilia inconstans* Fromentel, 1862.

Phragmosmilia lineata (Goldfuss, 1826) Pl. 6, fig. 2

- *1826 *Turbinolia lineata* Goldfuss: 108, pl. XXXVII, figs 18a–b.
- 1848 *Turbinolia lineata* Goldfuss; Milne Edwards & Haime, 3e sér., tome IX: 335.
- 1851 *Trochocyathus lineatus* (Goldfuss); Milne Edwards & Haime: 23.
- 1982 *Phragmosmilia lineata* (Goldfuss); Beauvais, tome I: 227–228, pl. XX, fig. 1 (older synonyms cited therein).
- v1998 *Phragmosmilia lineata* (Goldfuss); Baron-Szabo: 138, pl. 2, fig. 5.

MATERIAL. AZ 60.

MEASUREMENTS. d: 15 × 12 mm; s: ca. 80.

DESCRIPTION. The corallum is simple, trochoid and slightly elliptical in outline. Costosepta are compact and arranged in 5 nearly complete cycles and 6 systems, irregularly alternating in thickness. Their lateral surfaces are covered with spiniform or thick rounded granules, and with vertical carinae. Septa of the first two cycles and some of the third cycle extend to the axial region, where their inner ends may fuse with the columella. They are usually subequal in length but differ in thickness. Septa of the fourth cycle reach about three-quarters of the length of the preceding septa. The columella is thin and lamellar, discontinuous. Endotheca consists of numerous vesicular dissepiments. The wall is septothecal, but in places epithecal lamellae are present. Septal microstructure is poorly preserved. Frequently, minitrabeculae giving off secondary trabeculae can be seen.

OCCURRENCE. *Loftusia* beds (bed 7), SW corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Santonian-Campanian of Austria (Gosau Group), Campanian of northern Spain (Catalonia).

Suborder **DENDROPHYLLIINA** Vaughan & Wells, 1943

Family **DENDROPHYLLIIDAE** Gray, 1847

Genus **DENDROPHYLLIA** Blainville, 1830

TYPE SPECIES. *Madrepora ramea* Linnaeus, 1758.

Dendrophyllia nodosa Reuss, 1864 Pl. 7, figs 2–4

- *1864 *Dendrophyllia nodosa* Reuss: 26, pl. VII, figs 4–7.
- 1889 *Dendrophyllia nodosa* Reuss; Reis: 106.

1925 *Dendrophyllia nodosa* Reuss; Felix, pars 28: 163.

MATERIAL. AZ 562.

MEASUREMENTS. dl (max): 4–6.5 mm; dl (min): 2.5–5 mm; s: 32–46; size of the colony: 20 cm in diameter.

DESCRIPTION. Massive and fasciculate colony with corallites that are embedded in a vesicular, granulated coenosteum. Gemmation is due to extracalicular budding. Corallites are irregularly disposed over the colony, circular or elliptical in outline, and are monocentric or arranged in di- to tricentric groups. They are covered by concentric laminae, which vary in thickness. Costae are numerous and thin. Septa are thin, compact or subcompact, and arranged in 3 complete cycles with the beginning of a fourth cycle, irregularly following the Pourtalès plan. Up to 20 septa extend to the centre of the calice. Trabecular prolongations of their inner ends fill the axial region, sometimes fusing with the spongy columella. Lateral surfaces of septa have delicate spiniform and rounded granules. The wall is septoparathecal. Endotheca is well-developed and consists of subtabulate or cellular dissepiments. Septal microstructure is formed by simple minitrabeculae, sometimes giving off secondary ones. Granulations of the coenosteum are made of medium sized monaxial (and ?polyaxial) trabeculae.

REMARKS. In having a calicular diameter of around 3–6 mm, 3 cycles of septa in 6 systems with the beginning of a fourth cycle, and mono- to tricentric corallites that are irregularly disposed over the colony, the specimen from UAE/ Oman very closely corresponds to the original description and illustration of *Dendrophyllia nodosa* Reuss.

OCCURRENCE. East face of northernmost hill forming Jebel Buhays (loose, derived from lowest 3–4 m of section, beds 4–11), 4 km north of Al Madam.

DISTRIBUTION. Oliogocene of Austria.

Suborder **RHIPIDOGYRINA** Roniewicz, 1976

Family **RHIPIDOGYRIDAE** Koby, 1905

Genus **BARYSMILIA** Milne Edwards & Haime, 1848

TYPE SPECIES. *Dendrophyllia brevicaulis* Michelin, 1841.

Barysmilia irregularis (Reuss, 1854) Pl. 7, fig. 1

- v*1854 *Placocoenia irregularis* Reuss: 100, pl. IX, fig. 9.
- 1857 *Favia ? irregularis* (Reuss); Milne Edwards & Haime, vol. II: 437.
- 1861 *Favia ? irregularis* (Reuss); Fromentel: 173.
- 1899 *Favia ammergensis* Söhle: 45, pl. IX, figs 5, 5a.
- 1899 *Placocoenia irregularis* Reuss; Söhle: 51, pl. IX, figs 4, 4a, 4b.
- v1903a *Placocoenia irregularis* Reuss; Felix: 300, pl. XX, fig. 14, pl. XXV, fig. 4, text-fig. 51.
- 1914 *Placocoenia irregularis* Reuss; Felix, pars 7: 155.
- 1930 *Placocoenia irregularis* Reuss; Oppenheim: 408, pl. XXXIV, fig. 3.
- 1930 *Stenosmilia proletaria* Oppenheim: 437, pl. XLIII, fig. 3.

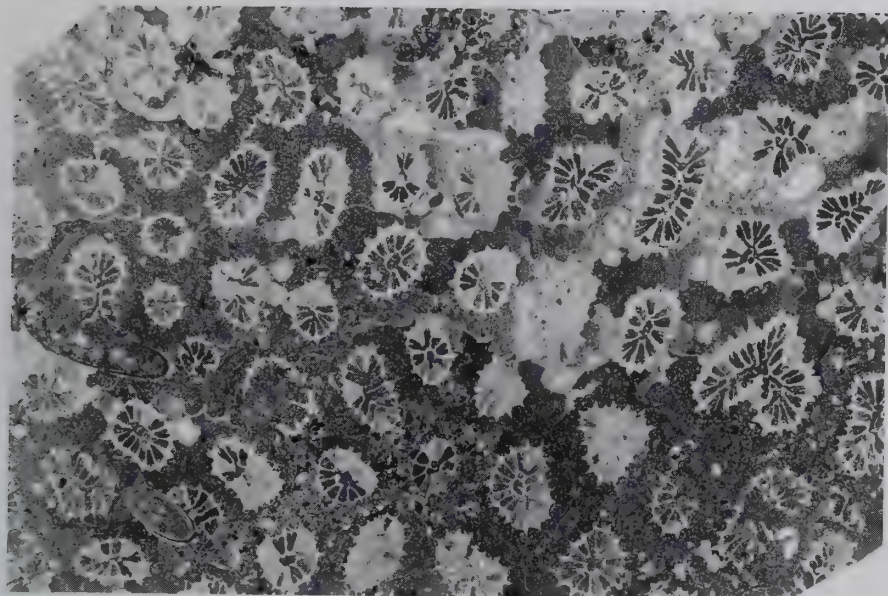
PLATE 7

Micrographs of plocoid (1) and plocoid-subfasciculate (2–4) coral colonies in transverse and longitudinal thin-sections.

Fig. 1 *Barysmilia irregularis* (Reuss, 1854); AZ 455.

Figs 2–4 *Dendrophyllia nodosa* Reuss, 1864; AZ 562.

Scale bar = 3 mm.



1



2



3



4

- v1934 *Dichocoenia trechmanni* Wells: 75, pl. 2, figs 7, 8.
 1957 *Dichocoeniopsis proletaria* (Oppenheim); Alloiteau: 265, pl. 16, figs 6, 7.
 v1982 *Barysmilia irregularis* (Reuss); Beauvais, tome I: 183, pl. XIV, fig. 10, pl. XV, fig. 1.

MATERIAL. AZ 454–55; AZ 635; AZ 637.

MEASUREMENTS. d (max) (monocentric calices): 3–5 mm; d (min) (monocentric calices): 2–3.5 mm; maximum diameter in late budding stages: up to 8 mm; c–c: 4–7 mm; s (monocentric calices): 15–27, up to about 50 in tricentric corallites; size of the colony: up to 15 cm in diameter.

DESCRIPTION. The corallum forms a massive or subfasciculate (no lateral connection of the some of the corallites), plocoid or subplocoid colony. Calices are slightly elongated or elliptical in outline. Increase is due to intra- and extracalicular budding, resulting in permanent monostomatous to tristomatous conditions. Costosepta are compact and non-confluent. They are arranged in 2 or 3, sometimes 4 cycles in 5, 6, 7, or 8 systems, occurring irregularly e.g. the first cycle consists of 5 septa, followed by 6 septa of the second cycle. Development of younger septal cycles is always influenced by corallite division. Septa of the first two cycles differ in thickness but are equal in length and extend to the centre of the calice where prolongations of their inner ends may fuse. Septa of younger cycles alternate in length and thickness. Free inner ends of septa of the first and second cycle are claviform or rhopaloid. Younger septa can have thickened or cuneiform inner ends. Septal flanks are covered mainly with spiniform, but also with rounded granules. The columella is lamellar or formed by twisted segments. The wall is septothecal or septoparathecal. The endotheca consists of thin cellular dissepiments. The exotheca is made of large vesicular dissepiments. In areas of incomplete separation of the corallites several calices can be directly united by their walls. The microstructure is poorly preserved, but in places centres of calcification can be seen, corresponding to the form of neorhipidacanth trabeculae.

OCCURRENCE. East face of most northern hill forming Jebel Buhays, 4 km north of Al Madam; outcrop at southern tip of Jebel Faiyah, 6 km NNE of Al Madam.

DISTRIBUTION. Lower Coniacian of France (Corbières), Santonian-Campanian of Austria (Gosau Group), Campanian-Maastrichtian of Jamaica.

Barysmilia iberica Baron-Szabo, 1998 Pl. 8, figs 1, 3

v*1998 *Barysmilia iberica* Baron-Szabo: 144, pl. 6, figs 1–3.

MATERIAL. AZ 361; AZ 568; AZ 644.

MEASUREMENTS. d (max): 1.8–3.5 mm; d (min): (*1.3) 1.8–2.2 mm; c–c: 2–3 mm; s: 14–26 (in late budding stages the number of septa may be larger); size of the colony: 5–20 cm in diameter.

DESCRIPTION. The corallum is in the form of a massive or subfasciculate (no lateral connection of the some of the corallites),

plocoid or subplocoid colony. Increase is by intracalicular budding, resulting in permanent monostomatous to distomatous, rarely tristomatous conditions. Costosepta are compact and non-confluent. They are arranged in 2 to 3 cycles in 5, 6, 7, or 8 equal or unequal systems. Septa of the first two cycles differ in thickness but can be equal in length. They extend to the centre of the calice where they may fuse with the columella. Younger septa are distinctly shorter and thinner. In general, inner ends of S_1 and S_2 are claviform or rhopaloid. Younger septa can have thickened or cuneiform inner ends. Septal flanks are covered with spiniform and rounded granules. The columella is lamellar and thin. The wall is septothecal or septoparathecal. The endotheca consists of thin tabulate and vesicular dissepiments. The exotheca is made of tabulate and slightly arched dissepiments. The microstructure is poorly preserved, but in places neorhipidacanth trabeculae can be seen.

OCCURRENCE. Main coral bed (*Loftusia* levels, bed 7), SW corner of Jebel Huwayyah, east of Al Ain; southern tip at Jebel Faiyah, 6 km NNE of Al Madam.

DISTRIBUTION. Campanian of northern Spain (Catalonia).

Genus *ORBIGNYGYRA* Alloiteau, 1952

TYPE SPECIES. *Diploria neptuni* d'Orbigny, 1850.

Orbignygyra salisburgensis (Milne Edwards & Haime, 1849) Pl. 8, fig. 2, Pl. 9, fig. 1

1845 *Meandrina tenella* Michelin: 293, pl. 66, fig. 5.

*1849 *Meandrina*? *saltzburgiana* Milne Edwards & Haime, 3. ser., tome XI: 283.

v1854 *Meandrina saltzburgiana* Milne Edwards & Haime; Reuss: 109, pl. XV, figs 12, 13.

1877 *Dendrogyra salisburgensis* (Milne Edwards & Haime); Fromentel: 440.

v1903a *Dendrogyra salisburgensis* (Milne Edwards & Haime); Felix: 306, pl. XXII, fig. 14, text-figs 54, 55.

non 1956 *Meandrina tenella* Michelin; Bendukidze: 89, pl. II, fig. 5.

1982 *Orbignygyra salisburgensis* (Milne Edwards & Haime); Beauvais, tome I: 204, pl. XVI, figs 4, 5, pl. LXIII, fig. 4 (older synonyms cited therein).

MATERIAL. AZ 584–85.

MEASUREMENTS. d (series): 4–8 mm; d (ambulacrum): 0.5–3 mm; s/ mm: 15–18/ 10; size of the colony: 15–25 cm in diameter.

DESCRIPTION. The corallum is a massive, meandroid colony with indistinct or subdistinct corallites, which are arranged in short sinuous series. Gemmation is due to intracalicular budding. Costosepta are compact, nonconfluent, and arranged in 3 size orders. Septa of the first order extend to the central region of the series. In general, their inner ends are claviform or rhopaloid, sometimes fusing with the columella. Septa of the second size order slightly alternate in

PLATE 8

Micrographs of plocoid (1, 3), meandroid (2), cerioid (4), and thamnasterioid (5) coral colonies in transverse and longitudinal thin-sections, and upper surface view.

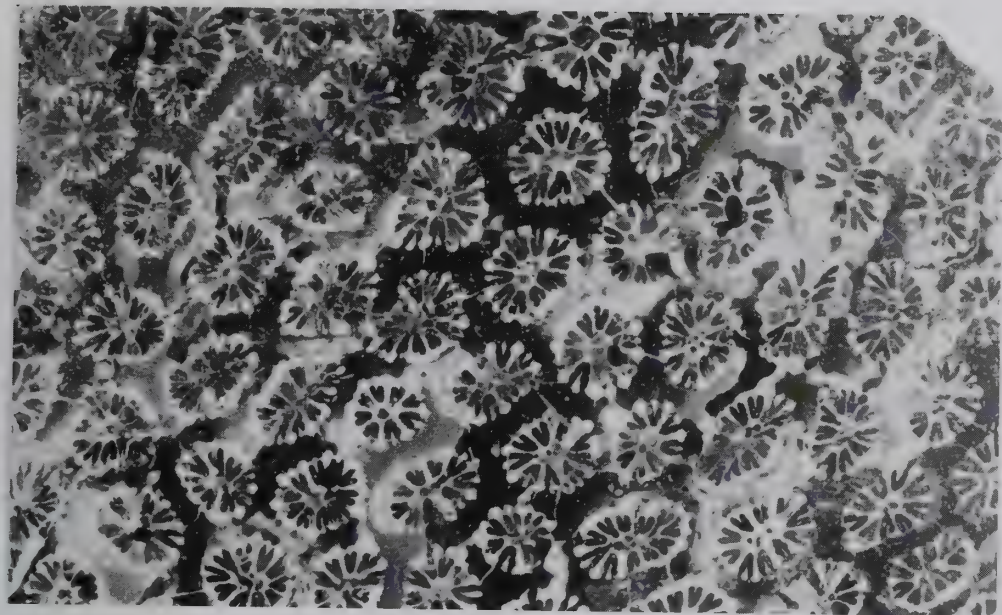
Figs 1, 3 *Barysmilia iberica* Baron-Szabo, 1998; AZ 361.

Fig. 2 *Orbignygyra salisburgensis* (Milne Edwards & Haime, 1849); AZ 584.

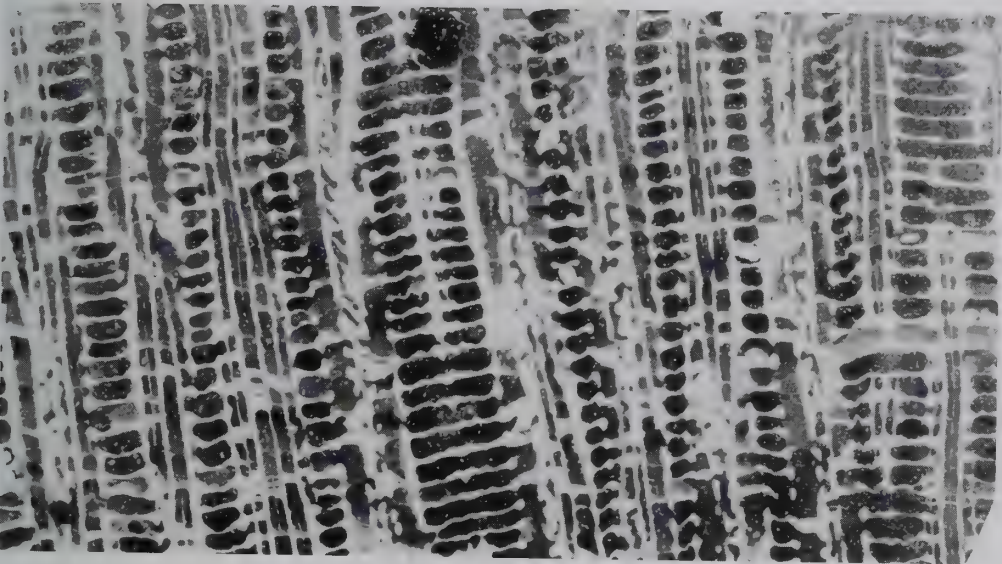
Fig. 4 *Pseudofavia grandiflora* (Reuss, 1854); AZ 406.

Fig. 5 *Astraraea multiradiata* (Reuss, 1854); AZ 409.

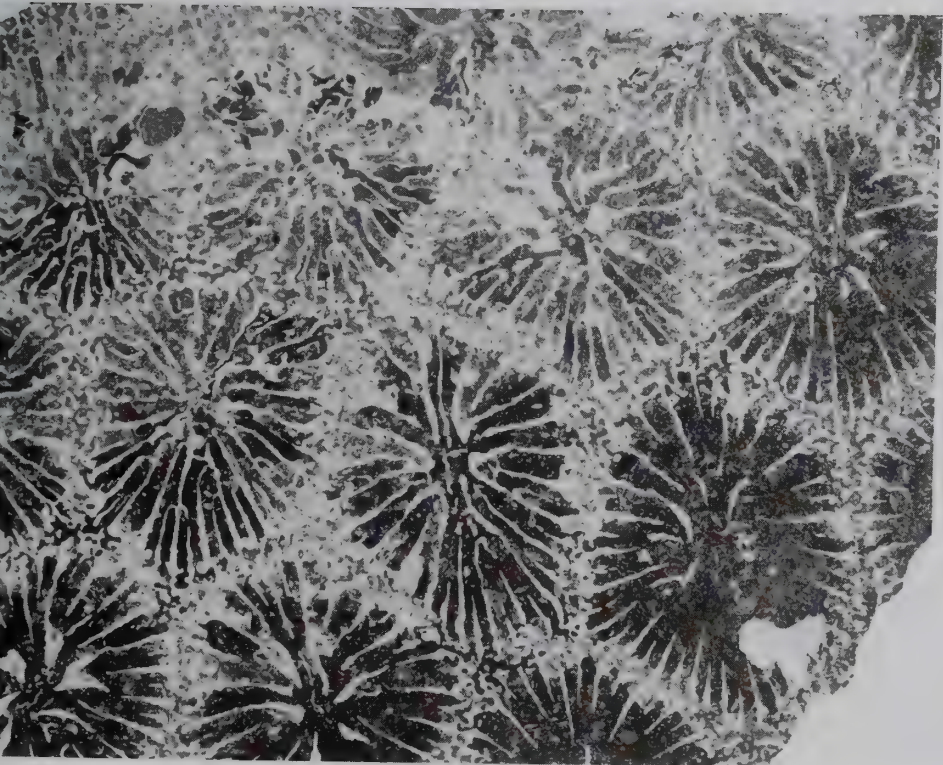
Scale bar = 3 mm.



1



3



4



2



5

length and thickness. Youngest septa are distinctly thinner and shorter. Lateral surfaces of septa are covered with rounded granules. The columella is lamellar, discontinuous. Wall is septothecal and parathecal. Endotheca consists of vesicular dissepiments, mainly occurring in the peripheral areas of the calicinal series.

REMARKS. The taxon *Meandrina tenella* Michelin (1845) represents a homonym of *Meandrina tenella* Goldfuss (1826). Therefore, the younger synonym by Milne Edwards & Haime (1849) has priority. In revising *Meandrina ? saltzburgiana* Milne Edwards & Haime, 1849, Fromentel (1877) grouped this form with the genus *Dendrogyra* and fully Latinized the species name to *salisburgensis*. According to the rules of nomenclature creating Latinized names for taxa is strongly recommended but it does not concern the validity of non-Latinized names. Therefore, the changes by Fromentel were not necessary. However, because the Latinized modification of the form by Milne Edwards & Haime has been constantly in use for over a century the author follows the rules of nomenclature in that a name is kept because it has been well known (Article 33.2.3.1); changing it back may cause confusion.

OCCURRENCE. Outcrop forming slope on south side of valley (bed 4), ca. 3 km east of Jebel Rawdah, east of Al Madam.

DISTRIBUTION. ?Senonian of Hungary, Santonian of Austria (Gosau Group), Upper Santonian of southern France (Corbières).

Suborder **FUNGIINA** Verrill, 1865

Family **HAPLARAEIDAE** Vaughan & Wells, 1943

Genus **ASTRARAEA** Felix, 1900

TYPE SPECIES. *Thamnastraea multiradiata* Reuss, 1854.

Astraraea multiradiata (Reuss, 1854) Pl. 8, fig. 5

- v*1854 *Thamnastraea multiradiata* Reuss: 118, pl. VII, fig. 1.
- 1858–61 *Synastraea multiradiata* (Reuss); Fromentel: 219.
- 1900 *Astraraea multiradiata* (Reuss); Felix: 38.
- v1903a *Astraraea multiradiata* (Reuss); Felix: 186, text-figs 10, 11.
- 1914 *Astraraea multiradiata* (Reuss); Felix, pars 7: 205.
- 1952a *Astraraea multiradiata* (Reuss); Alloiteau: 608, pl. II, fig. 9.
- 1982 *Astraraea multiradiata* (Reuss); Beauvais, tome II: 30, pl. XXIV, fig. 3, pl. XXV, fig. 1 (older synonyms cited therein).

MATERIAL. AZ 408–09.

MEASUREMENTS. c–c: 10–22 mm; s/ mm: 4–5/ 2; size of the colony: 3–7 cm in diameter.

DESCRIPTION. Massive, thamnasterioid colony with calices, which are regularly disposed. There are no corallite walls and septa are confluent between calices. Septa are subequal in thickness, irregularly perforated, and united by numerous synapticalae. About 30 septa extend to the columella. Septal flanks are covered with rounded

granules and pennulae. The columella is spongy-papillose, well-developed. Endotheca consists of vesicular or subtabulate dissepiments. Microstructure is made of monaxial and polyaxial thick trabeculae.

OCCURRENCE. Main coral bed (*Loftusia* levels, beds 3–8), SW corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Lower Coniacian of southern France (Corbières), Santonian of Austria (Gosau Group).

Genus **PSEUDOFAVIA** Oppenheim, 1930

TYPE SPECIES. *Parastraea grandiflora* Reuss, 1854.

Pseudofavia grandiflora (Reuss, 1854) Pl. 8, fig. 4

- v*1854 *Parastraea grandiflora* Reuss: 120, pl. XVI, fig. 10.
- v1903a *Parastraea grandiflora* Reuss; Felix: 181, fig. 7.
- 1930 *Pseudofavia grandiflora* (Reuss); Oppenheim: 65, pl. XL, fig. 5.
- 1943 *Pseudofavia grandiflora* (Reuss); Vaughan & Wells: 133, pl. 16, fig. 10.
- 1976 *Pseudofavia grandiflora* (Reuss); Turnšek, in Turnšek & Buser: 60, 81, pl. 18, figs 1–3.
- v1982 *Pseudofavia grandiflora* (Reuss); Beauvais, tome II: 16, pl. XXIII, fig. 3 (older synonyms cited therein).
- 1997 *Pseudofavia grandiflora* (Reuss); Turnšek: 174, figs 174 A–E.

MATERIAL. AZ 406.

MEASUREMENTS. d (max): 11–15 mm; d (min): 9–12 mm; c–c: 9–11; s: (*44) 48–60; size of the colony: about 9 cm in diameter.

DESCRIPTION. The corallum is in the form of a massive, cerioid colony. Corallites are polygonal in outline and separated by a vermiculate coenosteum, which is up to 2 mm in thickness. Septa are compact or subcompact, and arranged in 4 complete with the beginning of a fifth cycle in 6 systems. They regularly alternate in length, but can be nearly equal in thickness. Lateral surfaces of septa are covered by mostly delicate granules. Occasionally, thick rounded granules occur. Septa of the first two cycles reach the centre of the calice. Their inner ends may meet and fuse with the columella, or dissociate into paliform structures. Remaining septa alternate in length. The columella is spongy-papillose or consists of elongated segments. The occurrence of synapticalae is mainly restricted to both the peripheral areas of corallite and the peritheca. Wall is an incomplete paratheca or synapticulotheca. Endotheca is formed by subtabulate or vesicular dissepiments.

REMARKS. The description of the type of *Pseudofavia grandiflora* (Reuss) by Beauvais (1982, tome II: 16–17) disagrees with the type material in that it does not reflect the whole spectrum of variation in the specimen. Beauvais gives 21.5–35.5 mm for the calicular diameter, which corresponds to the largest corallites only (unpublished data, Baron-Szabo, 1995). In the type specimen corallites having a maximum diameter of (11) 15–22 mm are most common.

PLATE 9

Micrographs of meandroid (1), cerioid (2, 3), and branching phaceloid (4) coral colonies in transverse thin-sections.

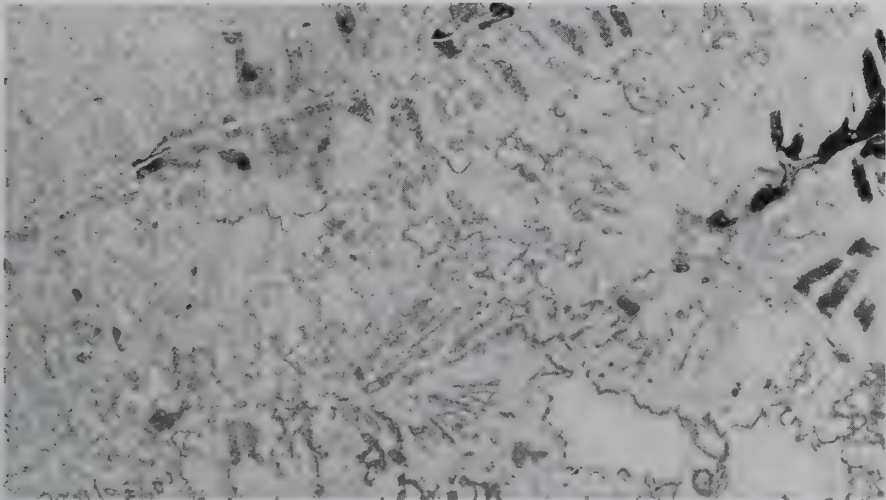
Fig. 1 *Orbignygyra salisburgensis* (Milne Edwards & Haime, 1849); AZ 584.

Fig. 2 *Goniopora elegans* (Leymerie, 1846); AZ 417.

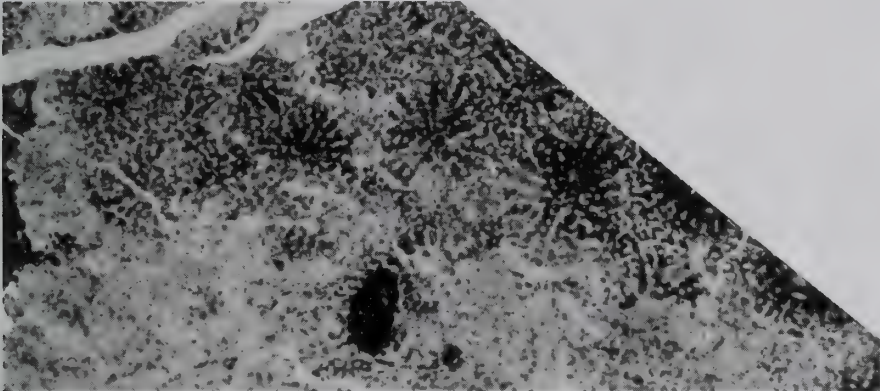
Fig. 3 *Goniopora imperatoris* Vaughan, 1919; AZ 415.

Fig. 4 *Calamophylliopsis simonyi* (Reuss, 1854); AZ 580.

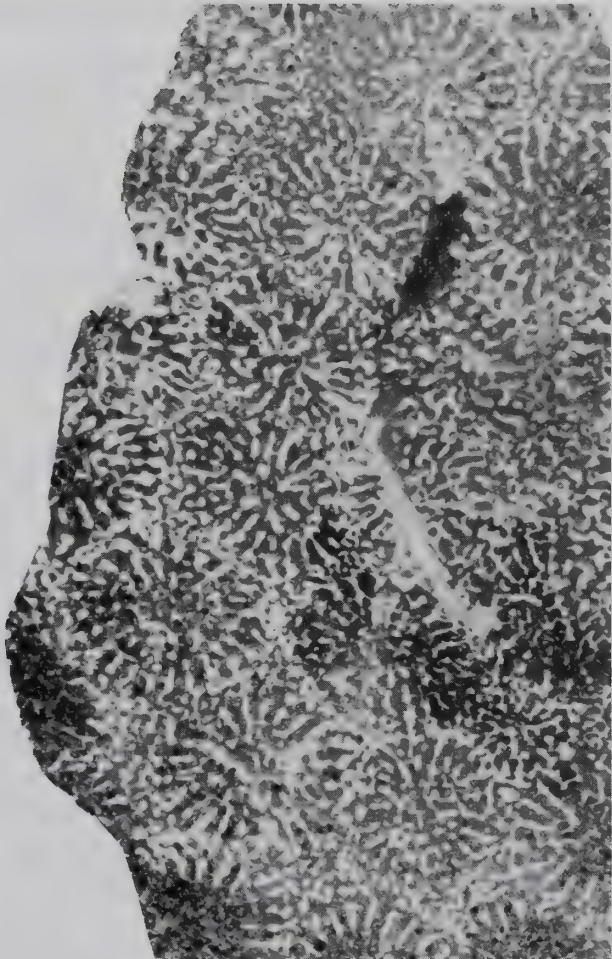
Scale bar = 3 mm.



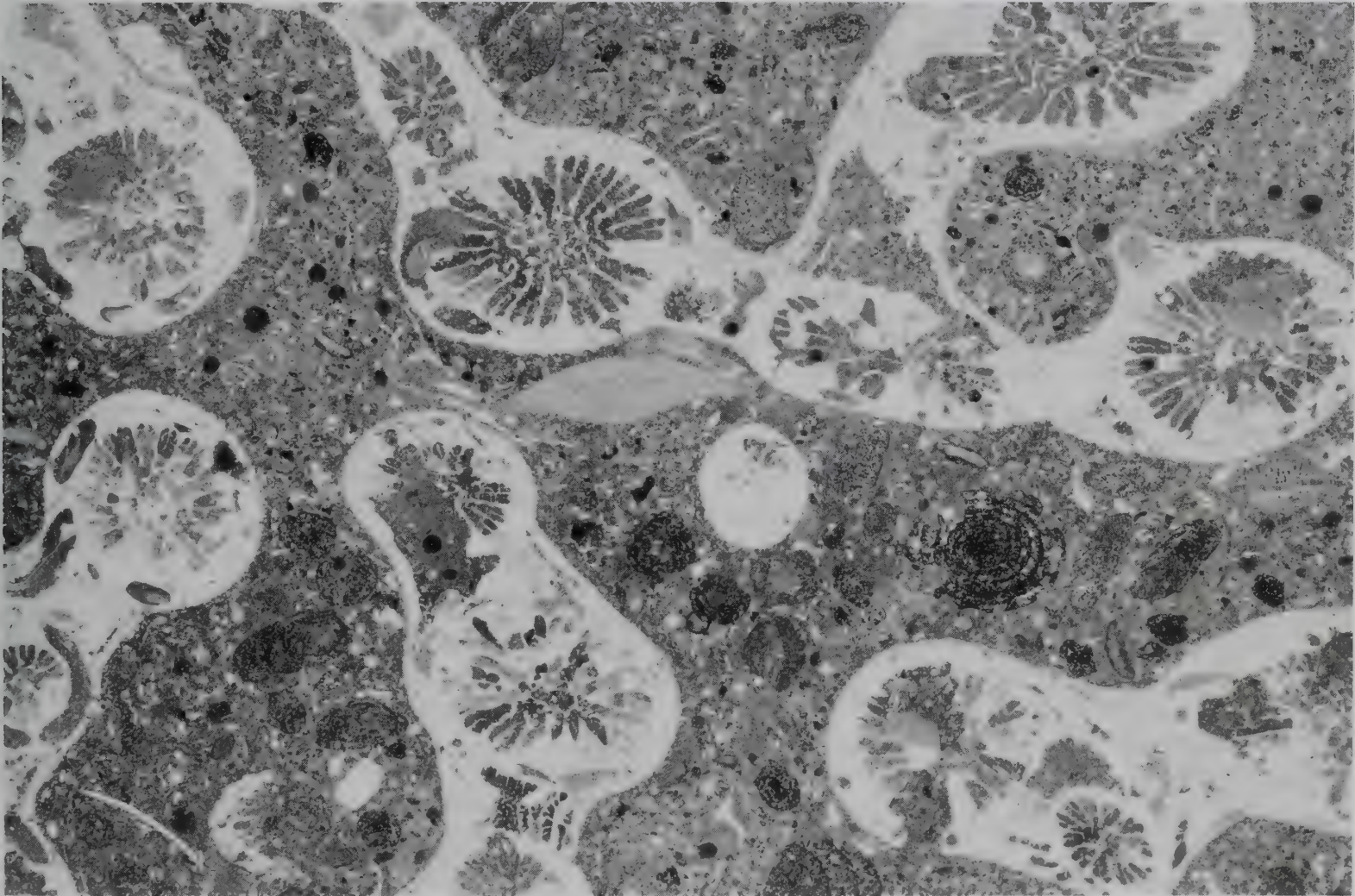
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3



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4

OCCURRENCE. SW corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Senonian breccia (redeposited) of Slovenia, ?Senonian of Georgia (in Caucasia), Santonian of Austria (Gosau).

Family **PORITIDAE** Gray, 1842
Genus **GONIOPORA** Blainville, 1830

TYPE SPECIES. *Goniopora pendunculata* Quoy & Gaimard in Blainville, 1830.

Goniopora elegans (Leymerie, 1846) Pl. 9, fig. 2

- *1846 *Porites elegans* Leymerie: 358, pl. 13.
- 1868 *Dictyaraea elegans* (Leymerie); Reuss: 163, pl. 15, figs 6, 7.
- 1882 *Litharaea* sp.; Pratz: 223.
- 1884 *Goniaraea elegans* (Leymerie); Felix: 424, pl. 3, figs 1, 2.
- 1912 *Goniaraea elegans* (Leymerie); Oppenheim: 98, pl. 12 (3), figs 2, 3, text-fig. 2.
- 1915 *Goniaraea elegans* (Leymerie); Dainelli: 216.
- 1942 *Goniaraea elegans* (Leymerie); Solè Sabaris: 398, pl. 8, fig. 52.
- 1987 *Goniopora elegans* (Leymerie); Kuzmicheva: 158, pl. XXVIII, fig. 7.
- 1988 *Goniopora elegans* (Leymerie); Drobne *et al.*: 188, pl. 34, figs 1–3.
- 1996 *Goniopora elegans* (Leymerie); Schuster: 73, pl. 15, fig. 4.

MATERIAL. AZ 412; AZ 416–17; AZ 419; AZ 960–61.

MEASUREMENTS. d: 2.5–4.5 mm; c–c: 3.5–6 mm; s: 20–24; size of the colony: about 8 cm in diameter.

DESCRIPTION. The corallum is massive with calices, that are rounded or irregularly polygonal in outline. Corallites are separated by a reticulated coenosteum. Septa are subcompact or porous, thin to moderate, nearly equal in thickness, and arranged in a bilateral system. Their lateral surfaces have delicate spiniform or rounded granules. About 10 septa reach the centre of the calice, where their inner ends may dissociate to form paliform structures or produce trabecular prolongations that join, or fuse with, the columella. Another order consisting of up to 10 septa reaches about half the length of S1, sometimes fusing with them. The columella is irregular spongy-papillose or formed by twisted segments. The wall is parathecal or synapticulothecal, incomplete. Endothecal dissepiments are rare. Thin synapticulae occur throughout the whole colony.

REMARKS. The specimens from the UAE/Oman very closely agree with the descriptions and illustrations of the forms listed in synonymy.

OCCURRENCE. Qahlah Formation, SW of Jebel Huwayyah, east of Al Ain; *Loftusia* bed (beds 3–8), SW corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Lower Paleocene of Croatia and the Ukraine, Eocene of Egypt, France, Bosnia, and Spain, Eocene-Lower Oligocene of Italy.

Goniopora imperatoris Vaughan, 1919 Pl. 9, fig. 3

- *v1919 *Goniopora imperatoris* Vaughan: 493, pl. 142, figs. 3, 3a.
- v1986 *Goniopora imperatoris* Vaughan; Foster: 85, pl. 35, figs. 3–7, pl. 36, figs. 1–7, pl. 37, figs. 1–4, text-figs. 2, 3, 6, 8, 11, 13, 14 (older synonyms cited therein).

MATERIAL. AZ 415; AZ 418; AZ 460.

MEASUREMENTS. d: (*1.5) 1.8–2.8 mm; c–c: (*2) 2.5–4 mm; s: 16–26; size of the colony: 8–10 cm in diameter.

DESCRIPTION. The corallum is massive, with calices that are rounded or polygonal in outline. Corallites are separated by a reticulated coenosteum. Septa are subcompact or porous, thin, nearly equal in thickness, and have delicate granulations laterally. Septal arrangement is bilateral. An order, consisting of about 8 septa, extends to the centre of the corallite, where the septa might dissociate to form paliform structures or trabecular prolongations, which join with the columella. A second order of about 8 septa reaches three-quarters the length S1. Youngest septa can be nearly equal with S2. Paliform structures irregularly occur axial to septa of every order. Columella is spongy or made of thin, twisted segments. Numerous synapticulae are scattered over the colony. The wall is synapticulothecal, incomplete. Endotheca consists of a few, thin dissepiments

REMARKS. The specimens from the UAE/ Oman closely correspond to the Tertiary forms of the Caribbean and Maastrichtian material from Jamaica (Baron-Szabo, in prep.).

OCCURRENCE. *Loftusia* bed (beds 3–8), SW corner of Jebel Huwayyah, east of Al Ain; loose, derived from lowest 3–4 m of section (beds 4–11), east face of most northern hill forming Jebel Buhays, 4 km north of Al Madam.

DISTRIBUTION. ?Upper Oligocene (Antigua Formation) of Antigua and ?Mexico (La Quinta Formation), Lower Miocene of Anguilla (Anguilla Formation) and ?Georgia (Chattahoochee Formation), Middle Miocene of Panama (La Boca Formation) and Puerto Rico (Ponce Formation), Lower Pliocene of the Dominican Republic.

Family **ACTINACIDIDAE** Vaughan & Wells, 1943
Genus **ACTINACIS** d'Orbigny, 1849

TYPE SPECIES. *Actinacis martiniana* d'Orbigny, 1849.

Actinacis parvistella Oppenheim, 1930 Pl. 11, figs 1, 3

- 1881 *Actinacis haueri* Reuss: Quenstedt, VI: 900, pl. 178, fig. 28.
- *1930 *Actinacis parvistella* Oppenheim: 9, pl. I, figs 3, 3a.
- 1930 *Actinacis multilamellata* Oppenheim: 13, pl. XV, fig. 2.
- v1933 *Actinacis valverdensis* Wells: 120, pl. 11, figs 1, 2.
- 1982 *Actinacis parvistella* Oppenheim; Beauvais, tome II: 273, pl. XLIX, figs. 1, 2, pl. LXIX, fig. 3.
- 1982 *Actinacis multilamellata* Oppenheim; Beauvais, tome II: 274, pl. XLIX, figs 3, 4, pl. LXIX, fig. 2.
- v1998 *Actinacis parvistella* Oppenheim; Baron-Szabo: 147, pl. 11, fig. 1.

MATERIAL. AZ 367; AZ 514; AZ 569; AZ 576; AZ 641; AZ 666; AZ 2528.

MEASUREMENTS. d: 0.8–1.2 (*1.5) mm; c–c: 1.5–3 mm; s: (*20–) 24; size of the colony: encrusting-lamellar: 35 × 12 mm; massive: 12–20 cm in diameter.

DESCRIPTION. The corallum forms an encrusting-lamellar or massive, plocoid colony. Circular or slightly oval calices have an average diameter of nearly 1 mm, and are separated by a vermiculate coenosteum. Costosepta, of which about 8 extend to the columella, are compact or subcompact, straight, nearly equal in thickness, but irregularly alternating in length. Anastomosis of septa is an irregular, but common feature. Paliform structures irregularly occur. All septa are thickened near the wall. Their lateral surfaces have spiniform

granulations. The columella is lamellar or formed by a few elongated segments. Numerous synapticulae are scattered throughout the colony. The wall is an incomplete (para-) synapticulotheca, made of one synapticular ring. Rare dissepiments are developed near the wall.

REMARKS. On the basis of the studies carried out by Beauvais (1982) the forms *Actinacis parvistella* Oppenheim and *Actinacis multilamellata* Oppenheim are considered to be synonymous. However, *Actinacis valverdensis* Wells closely agrees with both of these species.

OCCURRENCE. Main coral bed, *Loftusia* Levels (beds 7, 9), SW corner of Jebel Huwayyah, east of Al Ain; NE corner of Jebel Buhays, 4 km north of Al Madam; east face forming most northern hill of Jebel Buhays, 4 km north of Al Madam; outcrop at southern tip of Jebel Faiyah, 6 km NNE of Al Madam.

DISTRIBUTION. Middle Albian of Texas, Lower Coniacian of southern France, Upper Coniacian-Santonian of Austria (Gosau Group), Campanian of northern Spain (Catalonia).

Actinacis remesi Felix, 1903 Pl. 10, figs 3, 6

- *1903c *Actinacis remesi* Felix: 567, text-figs 1, 2.
- 1911 *Actinacis remesi* Felix; Trauth: 155, pl. IV, fig. 1, text-fig. 4.
- 1914 *Actinacis remesi* Felix; Felix, pars 7: 240.
- 1925 *Actinacis remesi* Felix; Vetter: 9, pl. I, figs 5, 6.
- non 1925 *Actinacis remesi* Felix; Kühn: 131.
- 1930 *Actinacis remesi* Felix; Oppenheim: 10, pl. XV, figs 3, 3a.
- ?1966 *Actinacis remesi* Felix; Morycowa & Lefeld: 538, pl. 33, figs 1, 2.
- 1976 *Actinacis remesi* Felix; Turnšek, in Turnšek & Buser: 63, 83, pl. 20, figs 5, 6.
- 1982 *Actinacis remesi* Felix; Beauvais, tome II: table 12.
- 1989 *Actinacis remesi* Felix; Eliasova: 96, pl. 50, figs 2, 3; pl. 56, fig. 3; pl. 59, figs 1, 2; pl. 60, fig. 1.

MATERIAL. AZ 570.

MEASUREMENTS. d: (*1.5) 1.8–2.5 mm; c–c: 2.5–4 mm; s: (*15) 17–22.

DESCRIPTION. Massive-lamellar and plocoid colony with corallites that are circular or elongated in outline. Calices are embedded in a very porous coenosteum. Costosepta are subcompact or porous, equal in thickness, with finely granulated lateral surfaces. In some calices a septal arrangement in 6 systems is perceptible. Paliform structures irregularly occur. The columella is made of a few papillae or twisted segments, sometimes uniting with inner ends of septa. Wall is an incomplete synapticulotheca. Endothecal dissepiments are thin, vesicular, and few in number. Synapticulae are disposed throughout the whole colony.

OCCURRENCE. NE side of Jebel Thanais, 4 km north of Al Madam.

DISTRIBUTION. ?Urgonian of Poland, Upper Cenomanian-Lower Santonian of the Czech Republic, Turonian-Senonian of Libya, Santonian-Campanian (Gosau Group) and Maastrichtian (northern alpine flysch) of Austria, redeposited in Senonian breccia of Slovenia.

Family ANDEMANTASTRAEIDAE Alloiteau, 1952
Genus BRACHYCOENIA Beauvais, 1982

TYPE SPECIES. *Adelastrea leptophylla* Reuss, 1854.

Brachycoenia leptophylla (Reuss, 1854) Pl. 11, fig. 2

- *1854 *Adelastrea leptophylla*: Reuss: 115, pl. XII, figs 3, 4.
- 1857 *Confusastraea leptophylla* (Reuss); Milne Edwards & Haime, tome II: 484.
- ?1956 *Confusastraea leptophylla* (Reuss); Bendukidze: 85, pl. IX, figs 2, 2a.
- 1982 *Brachycoenia leptophylla* (Reuss); Beauvais, tome II: 48, pl. XXVI, fig. 7, pl. XXVII, fig. 1 (older synonyms cited therein).
- v1999 *Brachycoenia leptophylla* (Reuss); Baron-Szabo: x, pl. 1, fig. 6, pl. 4, fig. 3.

MATERIAL. AZ 476.

MEASUREMENTS. c–c: 5–10 mm; s: 36–60, in late budding stages the number of septa may be larger; s/mm: 6–7/2; size of the colony: 7 cm in diameter.

DESCRIPTION. The massive and thamnasterioid colony has slightly protuberant calices, which appear to be subplocoid. Increase is due to intracalicular gemmation. Costosepta are subcompact or porous, confluent or subconfluent, nearly equal in thickness, and have pennulae and spiniform or coarse, rounded granules laterally. Their inner ends have a tendency to fuse. About 20 septa reach the centre of the calice. The columella is spongy-papillose, well-developed. Paliform structures can be frequently observed. Synapticulae are irregularly disposed. There is no wall between the corallites. Endotheca is formed by numerous vesicular or subtabulate dissepiments. Septal microstructure is made of thick monaxial and polyaxial trabeculae.

OCCURRENCE. SE corner of Jebel Huwayyah (beds 10/11), east of Al Ain.

DISTRIBUTION. ? Senonian of Georgia (in Caucasia), Upper Santonian-Campanian of Austria (Gosau Group).

Genus MESOMORPHA Pratz, 1882

TYPE SPECIES. *Porites mammillata* Reuss, 1854.

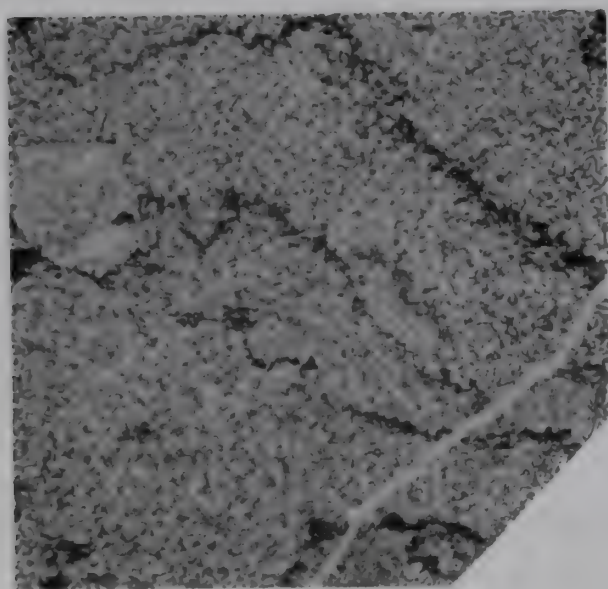
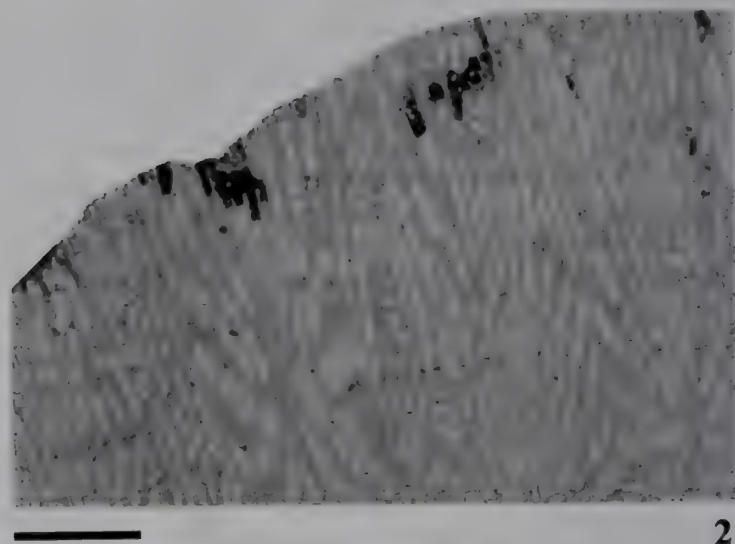
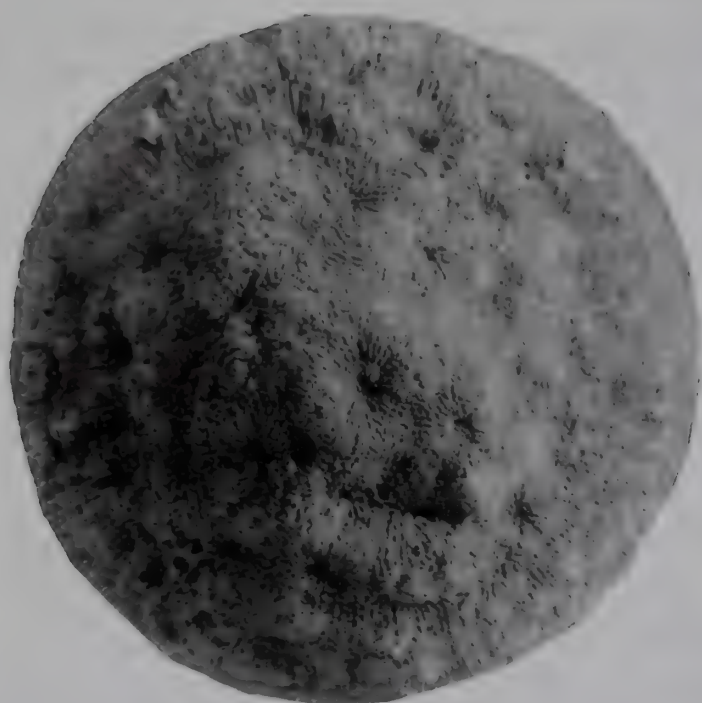
Mesomorpha mammillata (Reuss, 1854) Pl. 10, fig. 2, 8

- v*1854 *Porites mammillata* Reuss: 129, pl. X, figs 9, 10.
- 1860 *Coscinaraea mammillata* (Reuss); Milne Edwards, tome III: 204.
- 1882 *Mesomorpha mammillata* (Reuss); Pratz: 114.
- v1903a *Mesomorpha mammillata* (Reuss); Felix: 225.
- 1957 *Ahrdorffia mammillata* (Reuss); Alloiteau: pl. 4, fig. 10.
- v1982 *Mesomorpha mammillata* (Reuss); Beauvais, tome II: 61, pl. XXVI, fig. 5 (older synonyms are cited therein).

MATERIAL. AZ 904.

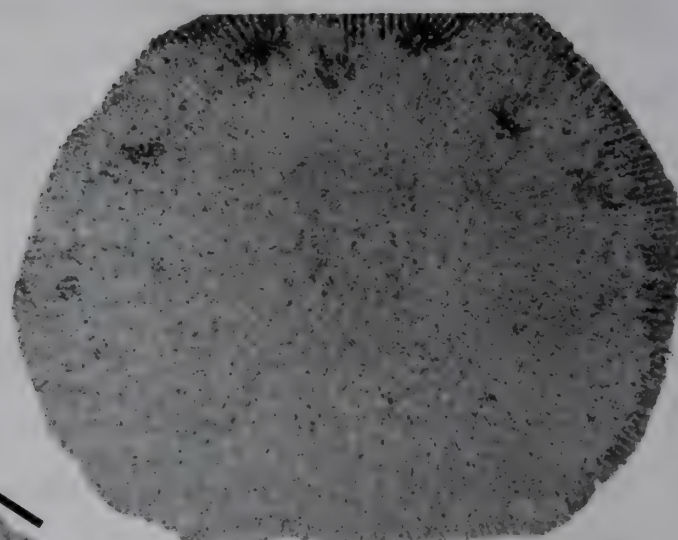
MEASUREMENTS. d: 2–2.5 mm, in later budding stages the corallite diameter can reach up to 3.5 mm; c–c: 2–4 mm; s: 18–24, in late budding stages the number of septa may reach 30; s/mm: 8–10/2; size of the colony: about 7 cm in diameter.

DESCRIPTION. Massive and thamnasterioid colony with corallites that appear to be polygonal in outline. Gemmation is due to intracalicular budding. Septa are compact, confluent, sub- or non-confluent, nearly equal in thickness, and finely granulated laterally. About 10 septa reach the centre of the calice, where they meet and fuse with the columella. Anastomosis is a common feature. The columella is styliform. Synapticulae are very abundant and occur

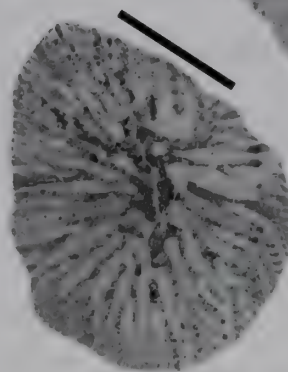


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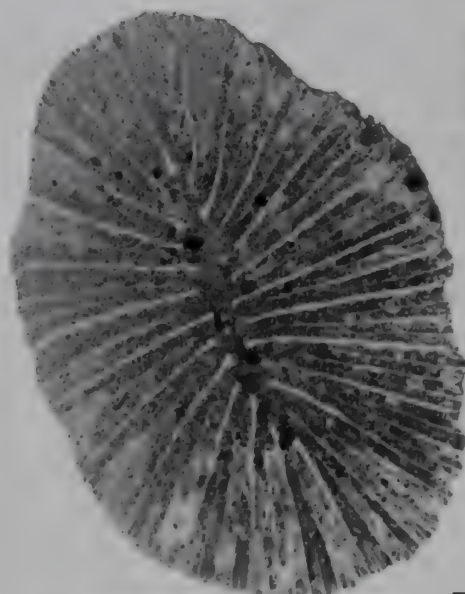
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7



8

throughout the whole colony. Endotheca consists of numerous thin, slightly arched or cellular dissepiments.

REMARKS. In the present specimen the majority of corallites is in condition of gemmation, resulting in a larger corallite diameter and a larger number of septa. However, in calices which are not influenced by budding the calicinal diameter is 2 mm and the number of septa is around 20, thus closely agreeing with the type material of *Mesomorpha mammillata* (Reuss). Another similar species represents the form *M. forojuiliensis* d'Archiardi, 1875, from the Eocene of Italy, with a corallite diameter of around 3 mm, but the number of septa can reach up to 60 in late budding stages.

OCCURRENCE. SE corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Lower Coniacian (Corbières, Aude) and Upper Santonian (Aude) of France, Santonian of Austria (Gosau Group).

Suborder **MICROSOLENINA** Morycowa & Roniewicz, 1995

Family **LATOMEANDRIDAE** Alloiteau, 1952

Genus **FUNGIASTRAEA** Alloiteau, 1952

TYPE SPECIES. *Astrea laganum* Michelin, 1841.

Fungiastraea crespoid (Felix, 1891) – Pl. 11, fig. 4

*1891 *Thamnastrea crespoid*: Felix: 146, pl. 22, fig. 5.

1963 *Thamnastreaa crespoid* Felix; Reyerros Navarro: 4, pl. 1, figs 1, 4.

1994 *Fungiastraea crespoid* (Felix); Löser: 66, pl. 9, fig. 4, pl. 11, figs 8, 9.

v1996 *Fungiastraea crespoid* (Felix); Baron-Szabo, in Baron-Szabo & Steuber: 27, pl. 16, figs 2, 3.

v1997 *Fungiastraea crespoid* (Felix); Sanders & Baron-Szabo: 74, pl. 21, fig. 8 (non fig. 7).

v1997 *Fungiastraea crespoid* (Felix); Baron-Szabo: 88, pl. 16, fig. 3.

v1999 *Fungiastraea crespoid* (Felix); Baron-Szabo & González-Léon: 490, figs 5(a), 6(i).

MATERIAL. AZ 642.

MEASUREMENTS. c–c: 4–8 mm; s/mm: 4–6/2; size of the colony: about 5 cm in diameter.

DESCRIPTION. The corallum is massive-lamellar and thamnasterioid. Septa are long, wavy, confluent, nearly equal in thickness, irregularly perforated, and have rounded or spiniform granules and pennulae laterally. The columella is spongy-papillose. A small number of synapticalae are irregularly distributed. The endotheca is made of thin tabulate and slightly arched dissepiments.

OCCURRENCE. *Loftusia* beds (beds 3–8), SW corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Lower Aptian of Austria and Germany (Allgäu Schrattenkalk), Aptian of central Greece, Aptian and Middle Albian of Mexico (Tehuacan, Sonora), Lower Cenomanian of northwestern

Germany, ?Upper Turonian-Lower Coniacian of Austria (Gosau Group).

Family **BRACHYPHYLLIIDAE** Alloiteau, 1952

REMARKS. Since its introduction by Alloiteau (1952a) the systematic position of the family Brachyphylliidae Alloiteau has been discussed. According to Alloiteau (1952a) and Beauvais (1982) this family belongs to the suborder Fungiina Verrill. Wells (1956) did not recognize Brachyphylliidae Alloiteau. However, on the basis of septal development, which seems to correspond closely to the microsolenid and latomeandrid types, the family Brachyphylliidae Alloiteau is grouped here with the suborder Microsolenina.

Genus **BRACHYPHYLLIA** Reuss, 1854

TYPE SPECIES. *Brachyphyllia dormitzeri* Reuss, 1954.

Brachyphyllia felixi sp. nov. Pl. 11, fig. 5

non 1848 *Pleurocora haueri* Milne Edwards & Haime, tome XI: 312.

non 1854 *Pleurocora haueri* Milne Edwards & Haime; Reuss: 112, pl. VI, figs 26, 27.

v*1903a *Brachyphyllia haueri* (Reuss); Felix: 261, pl. XX, fig. 15, text-fig. 29.

vnon 1903a *Pleurocora haueri* Milne Edwards & Haime; Felix: 261.

1905 *Brachyphyllia haueri* (Reuss); Angelis d'Ossat: 200.

pars 1914 *Brachyphyllia haueri* (Reuss); Felix, pars 5: 32.

non 1914 *Brachyphyllia haueri* (Reuss); Felix, pars 7: 170.

non 1914 *Pleurocora haueri* Milne Edwards & Haime; Felix, pars 7: 172.

1930 *Brachyphyllia haueri* Felix; Oppenheim: 343, pl. XLVI, figs 1–1b.

non 1978 *Pleurocora haueri* Milne Edwards & Haime; Turnšek, in Turnšek & Polšák: 155, 173, pl. 11, figs 1–3.

DERIVATIO NOMINIS. In honour of Prof Johannes Paul Felix.

HOLOTYPE. AZ 2527, from SE corner of Jebel Huwayyah, east of Al Ain.

PARATYPES. AZ 929; AZ 2529; AZ 2531; AZ 2537.

DIAGNOSIS. The species is characterized by the corallite diameter which ranges from 4–8 mm and the septal development of 4 to 5 complete septal cycles in 6 systems.

MEASUREMENTS. d: 4–8 (*10) mm; s: 60–up to ca. 100; size of the colony: up to 3 cm in diameter; single polyps in early settling stages: up to 8 mm in diameter.

DESCRIPTION. Plocoid colony with elevated corallites that are circular in outline. Gemmation is due to extracalicular budding. Costosepta are subcompact or compact in older cycles, straight, thin,

PLATE 10

Micrographs of thamnasterioid (1, 2, 4, 8), plocoid (3, 6), and trochoid (5, 7), coralla in transverse and longitudinal thin-sections, and upper surface view.

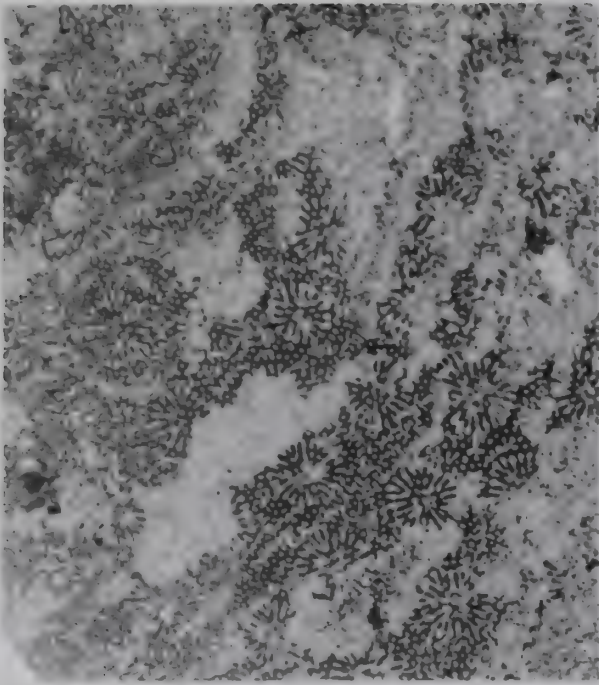
Figs 1, 4 *Aspidastraea orientalis* Kühn, 1933; 1, AZ 188; 4, AZ 636.

Figs 2, 8 *Mesomorpha mammillata* (Reuss, 1854); AZ 904.

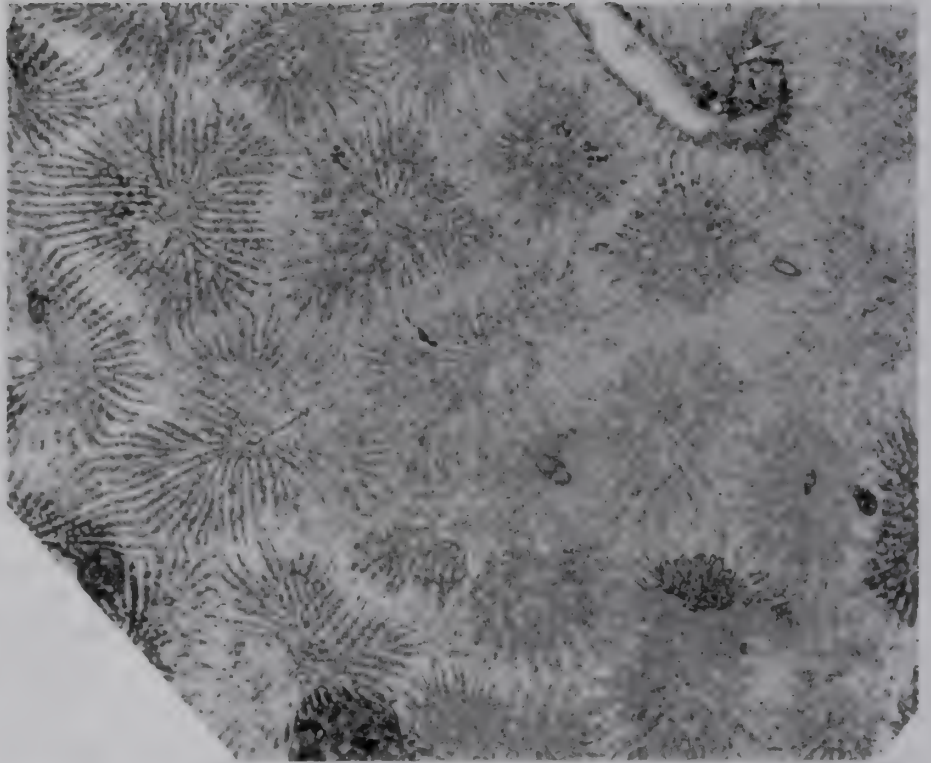
Figs 3, 6 *Actinacis remesi* Felix, 1903; AZ 570.

Figs 5, 7 *Trochocyathus microphytes* Felix, 1903; AZ 795; 5, juvenile stage.

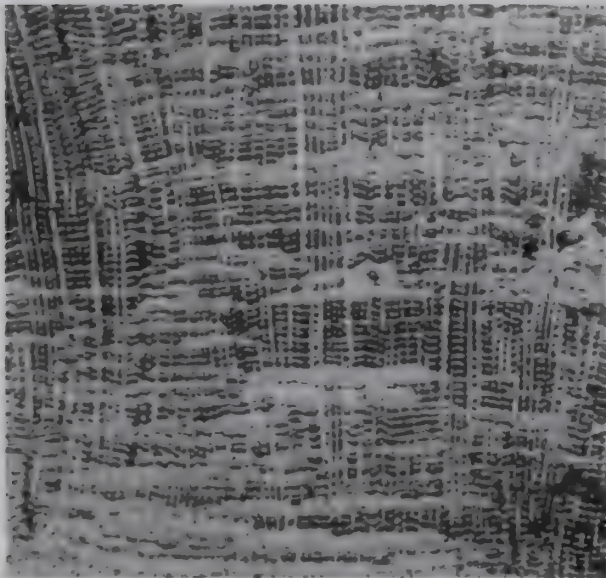
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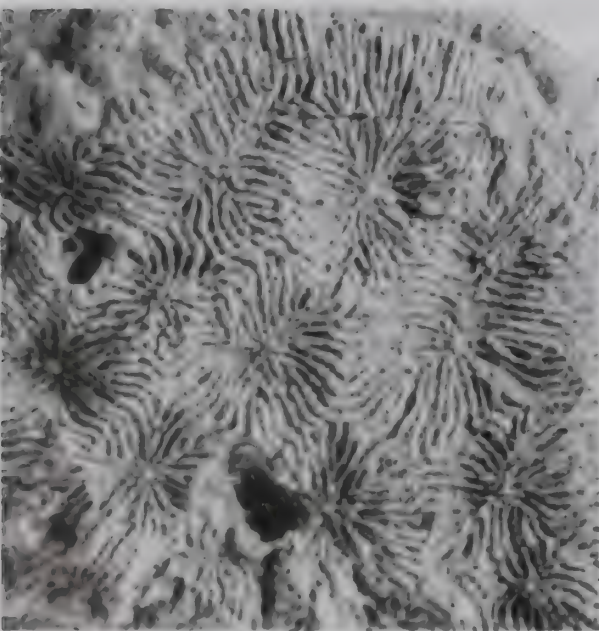
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5



4

and arranged in 4 to 5 cycles in 6 systems, regularly alternating in length. Septa of the first 3 cycles are nearly equal in thickness. Septa of remaining cycles are distinctly thinner. About 12 septa reach the axial region, sometimes fusing with neighbouring septa or with the spongy-papillose columella. Lateral surfaces of septa are covered by spiny or rounded granules and pennulae. Synapticulae are distributed throughout the colony. The wall is synapticulothecal. Endotheca consists of delicate vesicular dissepiments. In early ontogenetic stages the corallite may be covered by an epithecal wall.

COMPARISON. This new species is intermediate between *Brachyphyllia dormitzieri* Reuss, 1854, and *B. depressa* Reuss, 1854. From *B. dormitzieri* Reuss it is distinguished by the larger diameter of the corallites and the larger number of septa. In *B. dormitzieri* Reuss the corallite diameter ranges from 5 to 6 mm and the number of septa never exceeds 48, corresponding to 4 cycles in 6 systems. From *B. depressa* Reuss the new species differs by the smaller corallite diameter and the septal arrangement in up to 5 complete cycles in regularly developed 6 systems. In *B. depressa* Reuss the corallite diameter ranges from 13 to 18 mm and the septal apparatus follows the arrangement in 6 systems only in the first 4 cycles.

REMARKS. According to Felix (1903a: 261) the specimen that Reuss (1854: 112) assigned to *Pleurocora haueri* Milne Edwards & Haime represents a species of the genus *Brachyphyllia*. Instead of giving a new specific name, Felix just excluded Reuss's specimen from the synonymy of the species by Milne Edwards & Haime and referred to Reuss as first author, creating the form *Brachyphyllia haueri* (Reuss). Oppenheim's (1930) revision showed that *Brachyphyllia haueri* (Reuss) in Felix (1903a) did not correspond to *Pleurocora haueri* Milne Edwards & Haime in Reuss (1854). According to Oppenheim's studies Reuss's specimen represents a species of *Pleurocora*, but the form described by Felix belongs to the genus *Brachyphyllia*. Oppenheim tried to solve this problem by keeping the name of the taxon created by Felix (*Brachyphyllia haueri*) and naming him as first author of this species. However, because this is not an allowable taxonomic procedure, a new specific name has to be proposed.

OCCURRENCE. *Loftusia* beds, coral clast horizon, SE corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Aptian of northern Spain (Catalonia), Santonian-Campanian of Austria (Gosau Group).

Family CUNNOLITIDAE Alloiteau, 1952a

Genus CUNNOLITES Barrère, 1746

TYPE SPECIES. *Porpites ellipticus* Guettard, 1774 (= *Cyclolites elliptica* Lamarck, 1801).

Cunnolites sp.

Pl. 5, figs 2, 4

MATERIAL. AZ 98–101, AZ 103, AZ 107, AZ 109, AZ 113–14, AZ 116, AZ 128, AZ 135–38, AZ 140–42, AZ 147, AZ 150, AZ 153–54, AZ 159–60, AZ 169–70, AZ 207, AZ 215–16, AZ 220, AZ 222–24,

AZ 232–33, AZ 235–40, AZ 243, AZ 245, AZ 247, AZ 250–51, AZ 254, AZ 264–65, AZ 268, AZ 277–78, AZ 281–82, AZ 284, AZ 291, AZ 293–94, AZ 300–01, AZ 305–06, AZ 308–09, AZ 311, AZ 313, AZ 325, AZ 334, AZ 339, AZ 349, AZ 362, AZ 369–70, AZ 373, AZ 384, AZ 393–94, AZ 397, AZ 400, AZ 436, AZ 439–40, AZ 444–45, AZ 447, AZ 484–85, AZ 487–89, AZ 495, AZ 498–99, AZ 501, AZ 505a, AZ 506, AZ 508–11, AZ 519, AZ 640, AZ 740–41, AZ 743, AZ 746–47, AZ 749–50, AZ 752–53, AZ 755, AZ 758–60, AZ 762–63, AZ 766–67, AZ 769–71, AZ 773, AZ 775–77, AZ 779, AZ 803, AZ 805, AZ 807–08, AZ 817–19, AZ 821–23, AZ 826, AZ 830–31, AZ 834, AZ 837–41, AZ 844, AZ 846, AZ 851, AZ 853–61, AZ 864–70, AZ 872–74, AZ 877–78.

MEASUREMENTS. d (max) (D): 9–118 mm; d (min) (d): 9–80 mm; height of corallum (h): 3–30 mm; s/ mm (on upper surface of specimen, near central pit): 5/ 2; s/ mm (in peripheral areas of the specimen): 6–8 (*10)/ 2.

DESCRIPTION. The corallum is simple, free, circular or elliptical in outline. The base is flat or concave and can be partly or completely covered by a concentrically wrinkled epitheca. The corallum is convex above with an elongated or circular fossa. Septa are straight, moderate and subequal in thickness, porous or subcompact, and covered with numerous granules and pennulae laterally. According to the length 5 to 7 orders of septa can be distinguished. The density of septa varies from 5 in 2 mm in regions near the central pit to 6–8 (10) in 2 mm in peripheral areas. There is no columella. Thin endothecal dissepiments are present. Synapticulae are very abundant. The wall is synapticulothecal. Microstructure is poorly preserved, but in places thick compound trabeculae are present.

REMARKS. Studies on specimens of *Cunnolites* from the Campanian of Spain by Baron-Szabo (1998) showed that dimensions of skeletal elements cannot be used as specific characters for this genus, thus corresponding to the situation with *Diploctenium*. Therefore, the specimens of the UAE/ Oman are not assigned to any species. For further characterization of the population see Fig. 7.

OCCURRENCE. *Loftusia* Level, main coral beds (beds 5, 7, 10/ 11), Jebel Huwayyah, east of Al Ain; *Trigonia/ Pachymya* Bed, 3 km east of Jebel Rawdah, east of Al Madam, and below *Trigonia/ Pachymya* Bed (bed 9); Qahlah Formation, 16 km east of Madam Roundabout; main gastropod level (beds 7–8), north side of Jebel Bu Milh, 25 km NE of Hili; east face of most northern hill forming Jebel Buhays, 4 km north of Al Madam (loose beds 4–11); Simsim Formation or loose, derived from lowest 3–4 m of section, NE side of Jebel Thanais, 4 km north of Al Madam; SW corner (beds 3–5) and SE corner (bed 10, unit 9) of Jebel Huwayyah, east of Al Ain; Simsim Formation (Lower scree and higher), 3 km east of Jebel Rawdah, east of Al Madam; Simsim Formation (loose, from beds 18–19), 2 km east of Jebel Rawdah, east of Al Madam; Qahlah Formation, *Loftusia* Beds (beds 10/ 11), SE corner of Jebel Huwayyah, east of Al Ain; outcrop on east face, ca. 3 km north of the southern tip of Jebel Faiyah, NNE of Al Madam; base of Simsim Formation (bed 14), SE corner of Jebel Huwayyah, east of Al Ain; above *Zuffardia* level (beds 10–13, 15, 19), north side of valley, ca. 2 km east of Jebel

PLATE 11

Micrographs of plocoid (1, 3, 5) and thamnasterioid (2, 4) coral colonies in transverse and longitudinal thin-sections, and upper surface view.

Figs 1, 3 *Actinacis parvistella* Oppenheim, 1930; AZ 641.

Fig. 2 *Brachycoenia leptophylla* (Reuss, 1854); AZ 476.

Fig. 4 *Fungiastraea crespoid* (Felix, 1891); AZ 642.

Fig. 5 *Brachyphyllia felixi* sp. nov.; juvenile polyps in early settling stages of incipient colonies (arrow); AZ 2527.

Scale bar = 3 mm.

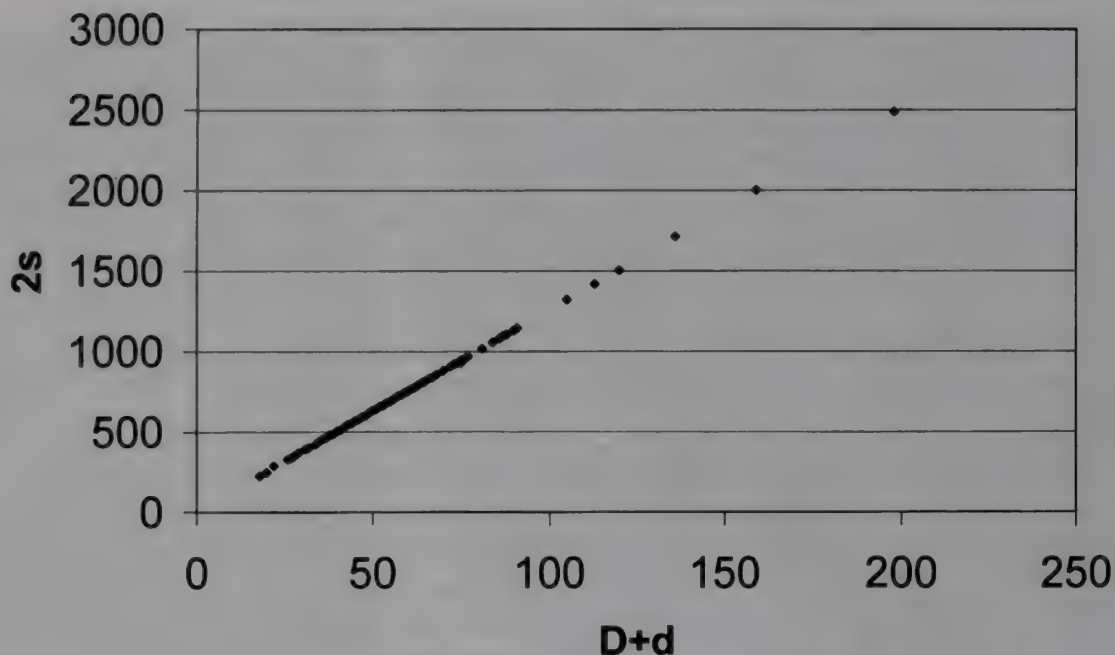


Fig. 7 The ratio of number of septa (2s) to the average diameter (D+d) for the specimens of *Cunolites* sp: the points form a single gradient suggesting that the population consists of a single species. However, according to the current classification, species of *Cunolites* also differ in height of corallum, size of calicular pit, etc., which obviously do not correspond to the number of septa nor to the size of the calicular diameter. Therefore, several species might be present in this population.

Rawdah, east of Al Madam; north side of valley, ca. 3 km east of Jebel Rawdah, east of Al Madam;

Genus *ASPIDASTRAEA* Kühn, 1933

TYPE SPECIES. *Aspidastraea orientalis* Kühn, 1933.

Aspidastraea orientalis Kühn, 1933 Pl. 5, fig. 6, Pl. 10, figs 1, 4

- v*1933 *Aspidastraea orientalis* Kühn: 179; pl. XVII, fig. 7.
 1943 *Aspidastraea orientalis* Kühn; Vaughan & Wells: 135.
 1952a *Aspidastraea orientalis* Kühn; Alloiteau: 668.
 1956 *Aspidastraea orientalis* Kühn; Wells: F387, fig. 280,3.
 1987 *Aspidastraea orientalis* Kühn; Kuzmicheva: 87, pl. V, fig. 5.

MATERIAL. AZ 156; AZ 176–81; AZ 184–202; AZ 211–12; AZ 252; AZ 336; AZ 348; AZ 496; AZ 636; AZ 812–14.

MEASUREMENTS. c–c (adjacent series): 3–5.5 (*7) mm; c–c (same series): (*1.5) 2.5–5 mm; 16–28, main corallite: up to 60; s/mm: 16–20/ 5; h: 5–25 mm; size of the colony: 18–53 mm in diameter.

DESCRIPTION. The corallum is in the form of a free colony, circular or slightly elliptical in outline. The base is flat or insignificantly concave, and is covered by a concentrically wrinkled epitheca. The corallum is convex above with corallites which are produced by circumoral budding. In general, one central calice is present, which appears to be larger. Rarely, two main calices may occur, or the size of the main calice might be reduced, closely corresponding to

dimension of the non-dominant corallites. Septa are straight or wavy, moderate and subequal in thickness, porous or subcompact, and covered with numerous granules and pennulae laterally. About 10 septa reach the centre of the calice. In the main calice up to 30 septa may extend to the axial region. The central part of the corallites can be free or filled with a trabecular columella. Thin endothecal dissepiments are present. Synapticalae are very abundant. There is no wall between the corallites.

REMARKS. The specimens of the UAE/ Oman very closely agree with the type material of *Aspidastraea orientalis* Kühn.

OCCURRENCE. NW end of Jebel Bu Milh (beds 3/ 4), 25 km NE of Hili; Simsima Formation (beds 15–19) or loose from middle part of section north side of valley, about 2 km east of Jebel Rawdah, east of Al Madam; east face of most northern hill forming Jebel Buhays (beds 4–11), 4 km north of Al Madam; above *Zuffardia* level (beds 13, 15, 19), north side of valley, ca. 2 km east of Jebel Rawdah, east of Al Madam; Simsima Formation (bed 15), 16 km east of Madam Roundabout; north side of valley, 3 km east of Jebel Rawdah, east of Al Madam.

DISTRIBUTION. Turonian of Armenia, Senonian of Iran.

Aspidastraea semhae (Kossmat, 1907) Pl. 12, figs 2, 4, 5

- *1907 *Aspidiscus semhae* Kossmat: 54, pl. V, figs 9a–c.
 1918 *Aspidiscus semhae* Kossmat; Fossa-Mancini: 145, pl. XIV [I], figs 10a, b.
 1922 *Aspidiscus semhae* Kossmat; Hoppe: 72.
 1930 *Aspidiscus semhae* Kossmat; Renz: 10.

PLATE 12

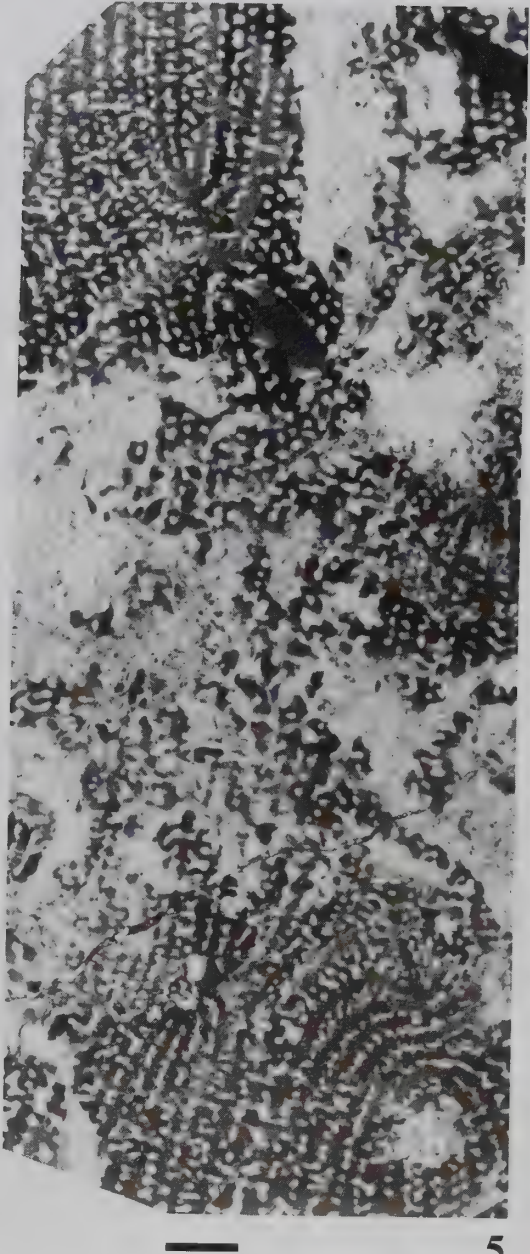
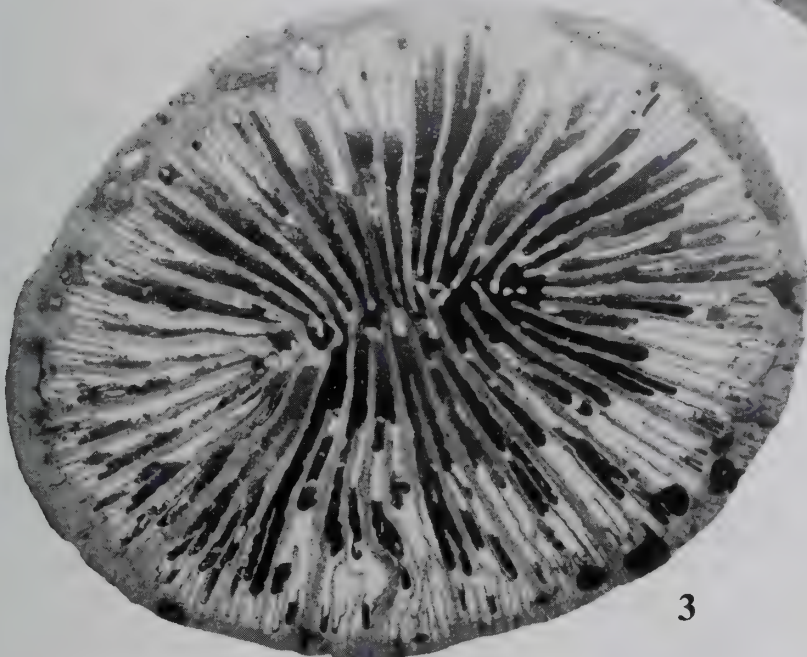
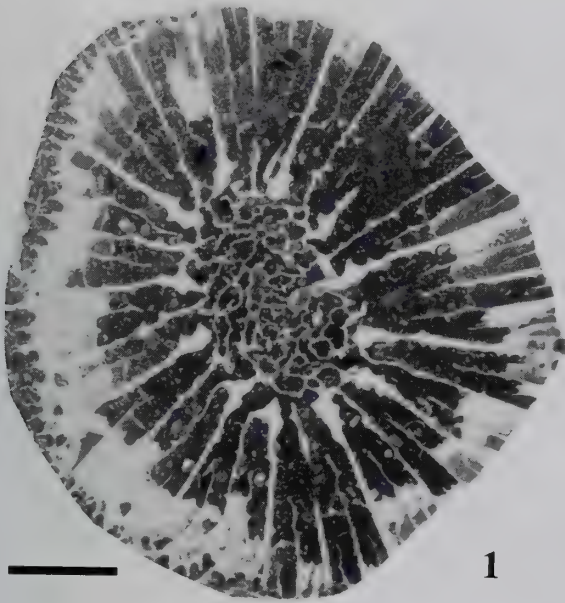
Micrographs of trochoid (1, 3) and thamnasterioid (2, 4, 5) coralla in transverse thin-sections and upper surface view.

Fig. 1 *Diegosmilia complanata* (Collignon, 1931); AZ 66.

Figs 2, 4, 5 *Aspidastraea semhae* (Kossmat, 1907); 2, juvenile form, AZ 407; 4, AZ 411; 5, AZ 572.

Fig. 3 *Trochocyathus microphytes* Felix, 1903; AZ 69.

Scale bar = 3 mm.



1931 *Aspidiscus semhae* Kossmat; Renz: 5.

1933 *Aspidastraea semhae* (Kossmat); Kühn: 180.

MATERIAL. AZ 402; AZ 407; AZ 411; AZ 572.

MEASUREMENTS. c-c (same series): 2–8 (*10) mm; c-c (adjacent series): 6–10 (*14) mm; s/mm: 9–12 (*16)/5; size of the colony: 3.5 × 4.5 cm to 13 × 23 cm.

DESCRIPTION. The corallum is in the form of a free colony, very elongated in outline. The base is flat or slightly concave, and can be covered by a smooth epitheca. The corallum is convex above. Corallites are arranged in circumoral rows. In general, no central calice is present. In juvenile forms slightly dominant central corallites may be present. Septa are thick, straight or wavy, equal in thickness, and porous or subcompact. Their lateral sides are covered with numerous pennulae and granules, varying in size and shape. Twelve to 24 septa reach the centre of the calice. The axial part of the corallites can be free or filled with a trabecular columella. The endotheca consists of thin dissepiments. Synapticulae are very abundant. There is no wall between the corallites. Microstructural features are not preserved.

OCCURRENCE. *Loftusia* Level, main corals bed, SW corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Cenomanian of the Arabian Gulf (Sokrota Island), Senonian of Iran.

Suborder CARYOPHYLLIINA Vaughan & Wells, 1943

Family PARASMILIIDAE Alloiteau, 1952

Subfamily PARASMILIINAE Vaughan & Wells, 1943

Genus DIEGOSMILIA Alloiteau, 1958

TYPE SPECIES. *Microseris complanata* Collignon, 1931.

Diegosmilia complanata (Collignon, 1931) Pl. 12, fig. 1

*1931 *Microseris complanata* Collignon: pl. V (I), figs 4–5b.

1958 *Diegosmilia complanata* (Collignon); Alloiteau: 153, pl. XXXIV, figs 5, 6, text-fig. 25.

MATERIAL. AZ 64; AZ 66.

MEASUREMENTS. d: 14–15 mm; s: 12s1+12s2+24s3+s; h: 35–50 mm.

DESCRIPTION. The corallum is simple and trochoid, circular in outline. Costosepta are compact, have spiniform and thick rounded granules laterally, and are arranged in 3 orders with the beginning of a fourth one. The first order consists of 12 thickest septa, extending to the centre of the calice. The second order, including 12 septa, can be equal in length but are distinctly thinner. The third order is formed by 24 septa, reaching about half or three quarters the length of the higher order septa. Last order septa are significantly thinner and shorter. The columella is irregularly spongy-trabecular and fused with trabecular prolongations of inner ends of septa of the first two orders. The wall is parathecal. Endotheca consists of vesicular dissepiments.

REMARKS. The specimens from the UAE/ Oman closely agree with the descriptions and illustrations of the type material in Alloiteau (1958: 153–154).

OCCURRENCE. *Loftusia* beds (beds 3–8), SW corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Cenomanian of Madagascar.

Family CARYOPHYLLIIDAE Dana, 1846

Subfamily CARYOPHYLLIINAE Milne Edwards, 1857

REMARKS. Commonly, Gray (1847) is being referred to as the first author to have described the family Caryophylliidae (e.g. Milne Edwards, 1857; Vaughan & Wells, 1943; Alloiteau, 1952). However, as pointed out by Cairns (1989) one year prior to Gray's work the family Caryophylliidae was created by Dana (1846: 364), thus giving the latter priority of authorship.

Genus TROCHOCYATHUS Milne Edwards & Haime, 1848

TYPE SPECIES. *Turbinolia mitrata* Goldfuss, 1826.

REMARKS. The variability of a large number of characteristics (e.g. columella, pali, thickness of septa) in the genus *Trochocyathus* was previously recognized by Milne Edwards & Haime (1848: 300). Later, Alloiteau (1958) used these features to divide *Trochocyathus* into three independent groups: *Trochocyathus*, *Protrochocyathus*, and *Paratrochocyathus*. According to Kühn (1966: 339) these characteristics are not sufficient for separation at genus level. Recent studies carried out by Cairns (1997) support this idea. Based on cladistic analysis on turbinoliid genera Cairns (1997) concluded that less taxonomic weight should be given to characters such as columella and pali. These results suggest that those skeletal elements are of minor taxonomic value, thus strongly agreeing with the idea proposed for *Trochocyathus* by Milne Edwards & Haime. Therefore, the author considers *Protrochocyathus* Alloiteau and *Paratrochocyathus* Alloiteau as younger synonyms of *Trochocyathus* Milne Edwards & Haime.

Trochocyathus microphyes Felix, 1903

Pl. 10, figs 5, 7, Pl. 12, fig. 3

*1903a *Trochocyathus microphyes* Felix: 354, pl. XVIII, figs 9, 10.

1914 *Trochocyathus microphyes* Felix; Felix, pars 7: 209.

1930 *Trochocyathus micraphye* Felix; Oppenheim: 548.

MATERIAL. AZ 61; AZ 63; AZ 69–70; AZ 77; AZ 81; AZ 482; AZ 780–83; AZ 786; AZ 792–93; AZ 795.

MEASUREMENTS. d (max) (D): 22–41 mm; d (min) (d): 17–30 mm; s: 120–180; h: 25–65 mm; d/D: 0.7–0.89; juvenile stage (measured in about 4 mm height): d: 4–7 mm; s: 48 (12+12+24).

DESCRIPTION. The corallum is simple and turbinate, trochoid or ceratoid. The corallite is elongated or compressed. Costosepta are compact, thin or moderate, straight or slightly curved, finely granulated laterally, and arranged in 5 complete with the beginning of a

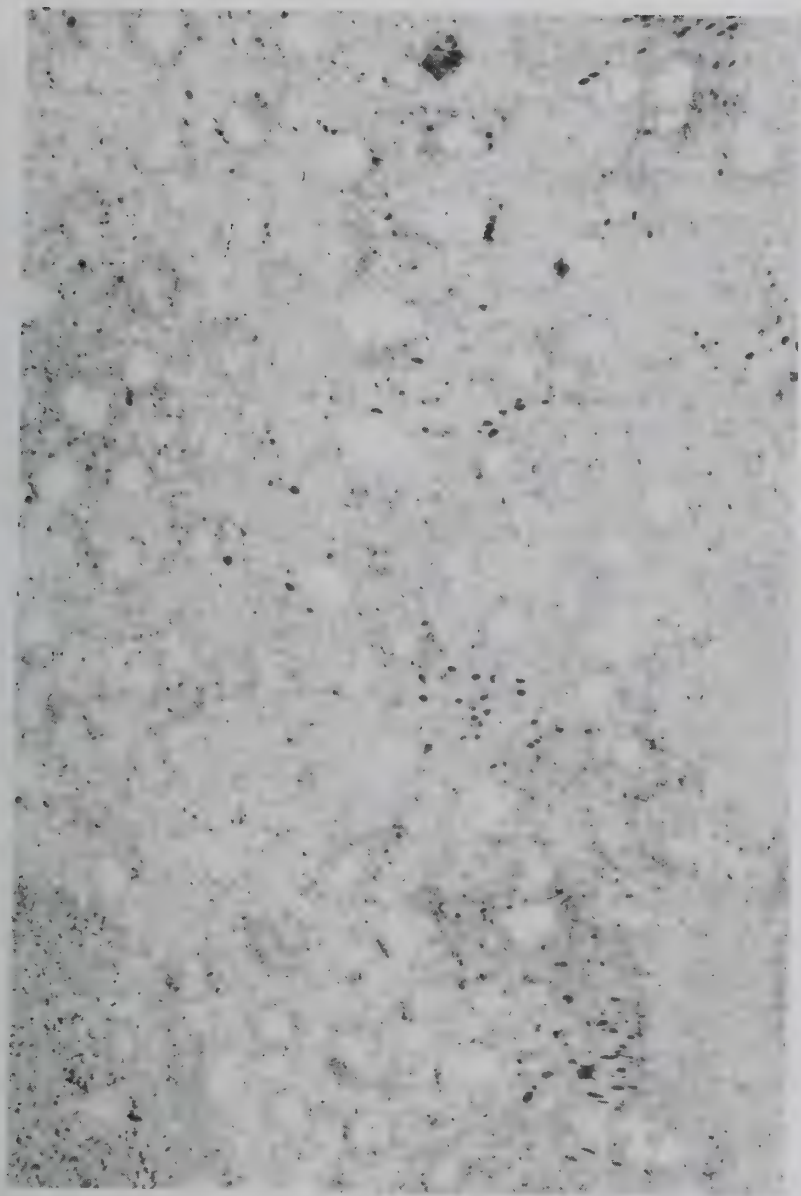
PLATE 13

Micrographs of massive octocorals with calicinal tubes in transverse (1, 4) and longitudinal (2, 3) thin-sections.

Figs 1, 2 *Polytremacis edwardsana* (Stoliczka, 1873); AZ 561.

Figs 3, 4 *Polytremacis blainvillei* (Michelin, 1841); AZ 965.

Scale bar = 3 mm.



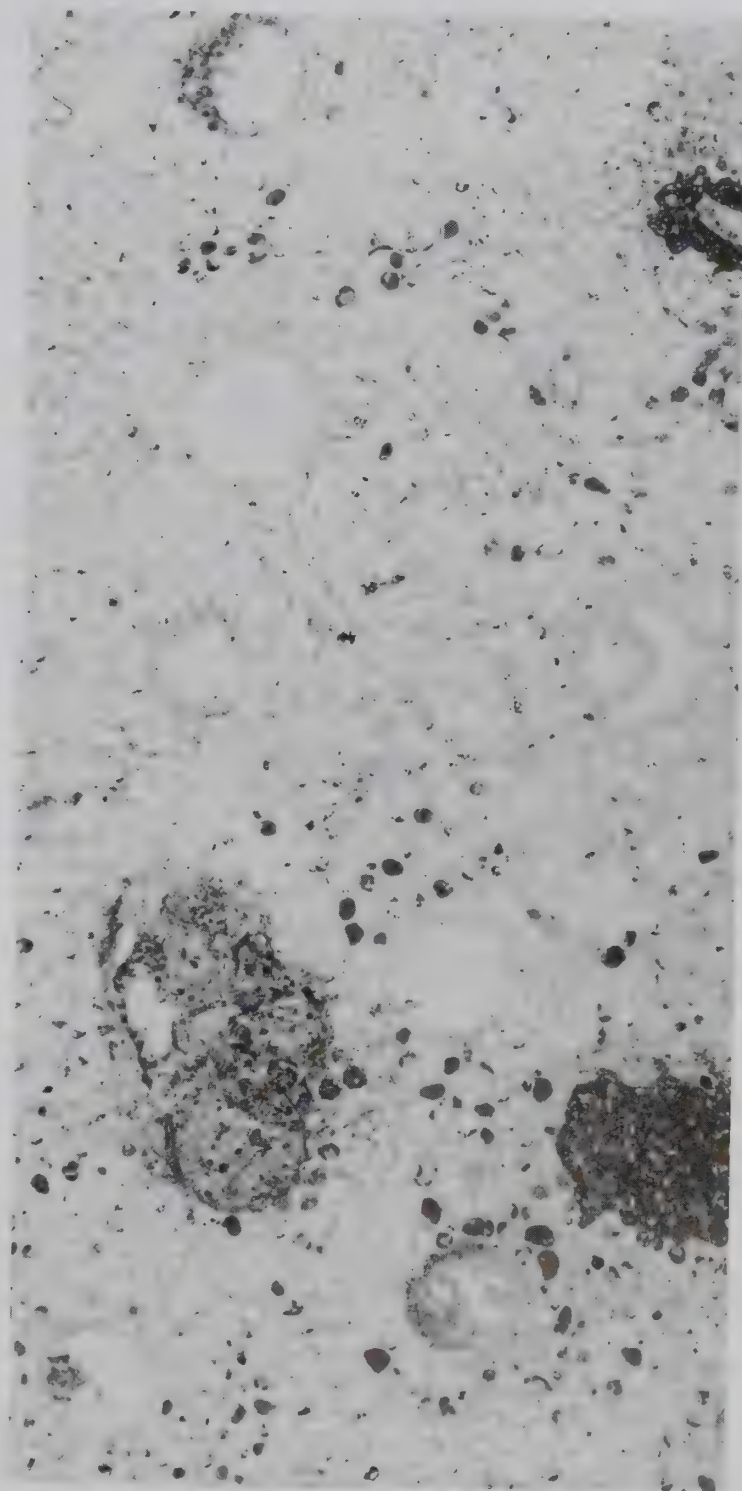
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2



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4

sixth cycle in 12 systems. In general, septa regularly alternate in thickness. Inner ends of septa of the first 3 cycles terminate in very elongated paliform structures. In younger septa development of paliform features may be perceptible or not present. The columella is very variably shaped: spongy-papillose, or fused papillae may form elongated segments, or it may be very weakly developed (trabecular). Wall is septothecal. Endotheca consists of vesicular dissepiments.

REMARKS. The juvenile stage of the specimens (measured in about 4 mm height of the coralla) very closely correspond to the description and illustration of *Trochocyathus microphytes* Felix, which has a calicular diameter of 5 mm and a height of 3 mm. It is suggested that the specimens of the UAE/ Oman represent ontogenetically older stages of this species. The nature of the very elongated paliform structures have been previously well illustrated by Alloiteau (1958: 131, fig. 21; Baron-Szabo, 1998: pl. 7, fig. 4).

OCCURRENCE. Qahlah Formation, *Loftusia* beds, SW corner of Jebel Huwayyah, east of Al Ain.

DISTRIBUTION. Santonian of Austria (Gosau Group)

Subclass **OCTOCORALLIA** Haeckel, 1866
Order **COENOTHECALIA** Bourne, 1900
Family **HELIOPORIDAE** Moseley, 1876
Genus **POLYTREMACIS** d'Orbigny, 1849

TYPE SPECIES. *Heliopora blainvilleana* Michelin, 1841.

Polytremacis blainvillei (Michelin, 1841) Pl. 13, figs 3, 4

- *1841 *Heliopora blainvilleana* Michelin: 27, pl. VII, fig. 6a, b.
- 1850 *Polytremacis blainvilleana* (Michelin); d'Orbigny, tome II: 209.
- non 1854 *Polytremacis blainvilleana* (Michelin); Reuss: 131, pl. XXIV, figs 4–7.
- non 1903a *Polytremacis blainvilleana* (Michelin); Felix: 356.
- non 1956 *Polytremacis blainvilleana* (Michelin); Bendukidze: 119.
- 1957 *Polytremacis blainvillei* (Michelin); Alloiteau: 378–381.

MATERIAL. AZ 459; AZ 525; AZ 527; AZ 588; AZ 885; AZ 930; AZ 965.

MEASUREMENTS. d: (*0.8) 1.1–1.6 (*1.8) mm; c–c: 1.5–5 mm; s: 14–18 (21); tubes/ mm²: 17–21; size of the colony: 3–20 cm in diameter.

DESCRIPTION. The colony is massive or nodular. Calicinal tubes are circular or slightly elongated in outline and imbedded in a vermiculate exoskeleton, composed of very small rounded or elliptical tubes. Septa are very short and thorn-like. Calicular tabulae are well-developed, tabulate or slightly arched.

REMARKS. According to Beauvais (1982, tome I: 39), in having a very unequally developed septal apparatus with generally large septa the specimens assigned to *Polytremacis blainvilleana* (Michelin) by Reuss (1854), Felix (1903a), and Bendukidze (1956) represent forms of the genus *Parapolytremacis* Alloiteau (1957: 381).

OCCURRENCE. *Loftusia* Beds, Qahlah Formation, east side of U-shaped Jebel, 10 km NE of Al Ain; east face of most northern hill forming Jebel Buhays, 4 km north of Al Madam, partly loose, derived from 3–4 m of section (beds 4–11); *Loftusia* Beds, Qahlah

Formation, SE corner of Jebel Huwayyah, east of Al Ain; outcrop at southern tip of Jebel Faiyah, 6 km NNE of Al Madam.

DISTRIBUTION. Turonian of France.

Polytremacis edwardsana (Stoliczka, 1873) Pl. 13, figs 1, 2

- *1873 *Heliopora edwardsana* Stoliczka: 53, pl. XI, fig. 11.
- 1900 *Heliopora edwardsi* Stoliczka; Gregory: 299.
- 1911 *Heliopora tenera* Trauth: 169, text-fig. 6, pl. IV, fig. 3.
- 1914 *Heliopora edwardsi* Stoliczka; Felix, pars 6: 141.
- 1914 *Heliopora tenera* Trauth; Felix, pars 7: 248.
- 1936 *Heliopora edwardsana* Stoliczka; Hackemesser: 76, pl. 6, fig. 11.
- 1964 *Polytremacis edwardsana* (Stoliczka); Morycowa: 55, pl. XII, figs 1a–e.
- 1971 *Polytremacis tenera* (Trauth); Morycowa: 136, fig. 41, pl. XL, fig. 1.
- 1981 *Polytremacis edwardsana* (Stoliczka); Scott: 465.
- 1982 *Polytremacis tenera* (Trauth); Beauvais, tome III: 36, pl. LIII, fig. 7, pl. LVIII, fig. 5.
- 1997a *Polytremacis edwardsana* (Stoliczka); Eliášová: 69, pl. VIII, figs 1, 2.
- v1998 *Polytremacis edwardsana* (Stoliczka); Baron-Szabo: 154, pl. 1, fig. 7.

MATERIAL. AZ 561; AZ 886.

MEASUREMENTS. d: 0.6–0.9 (*1.1) mm; c–c: 1.5–4 mm; s: 14–18; tubes/ 1 mm²: 19–25; size of the colony: up to 15 cm in diameter.

DESCRIPTION. The colony is massive, knobby or lamellar, with calicinal tubes which are circular or slightly elongated in outline. They are embedded in a vermiculate exoskeleton, composed of very small rounded or elliptical tubes. Septa are very short and thorn-like. Calicular tabulae are well-developed and slightly arched.

REMARKS. The descriptions and illustrations of the species *Polytremacis tenera* (Trauth) closely agree with *Polytremacis edwardsana* (Stoliczka), suggesting that they are synonymous. Moreover, the specimens described from Spain (Baron-Szabo, 1998) as well as the specimens at hand unite characteristics of both species.

OCCURRENCE. East face of most northern hill forming Jebel Buhays, 4 km north of Al Madam.

DISTRIBUTION. Barremian–Lower Aptian of Poland, Lower Aptian of Romania, Lower Albian of Mexico and Arizona (Mural Limestone), ?Cenomanian of Greece, Cenomanian (?–Turonian) of India, Upper Cenomanian and Senonian of the Czech Republic, Santonian–Campanian of Austria (Gosau Group), Upper Santonian of southern France, Campanian of northern Spain (Catalonia).

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Rhombocladia dichotoma (M'Coy, 1844) [Fenestrata, Bryozoa]: designation of a lectotype

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SYNOPSIS. A lectotype (National Museum of Ireland, NMING:F7058) from the Viséan of Black Lion, near Enniskillen, County Cavan, is designated for the fenestrate bryozoan *Rhombocladia dichotoma* (M'Coy, 1844).

In 1996 I published a paper that described a diverse Lower Carboniferous bryozoan fauna from the Viséan of County Fermanagh, Ireland (Wyse Jackson 1996). In that paper an important error in relation to the designation of a lectotype for the fenestrate bryozoan *Rhombocladia dichotoma* (M'Coy, 1844) inadvertently occurred.

This species was first described as *Vincularia dichotoma* from the Carboniferous of Ireland (M'Coy, 1844). Comparison of M'Coy's fourteen extant syntypes with material from County Fermanagh, resulted in the species being reassigned to the fenestrate genus *Rhombocladia* Rogers, 1900 (Wyse Jackson 1996: 144), a genus previously reported only from the United States, Russia, the Carnic Alps, and Western Australia.

As M'Coy failed to indicate which specimen was the holotype of the species, a lectotype for *Rhombocladia dichotoma* (M'Coy, 1844) was designated from his syntype suite (Wyse Jackson 1996: 144). In doing so the other specimens automatically became paralectotypes. The specimen designated lectotype was NMING:F7058 from the Asbian of Black Lion, Co. Cavan, Ireland (Griffith Collection, National Museum of Ireland [NMING]). This specimen was not illustrated by me. The specimen (NMING:F6030) illustrated in the paper (Wyse Jackson, 1996: fig. 57) (also a syntype from the Griffith Collection) was correctly referred to in the text as being a paralectotype.

However, a serious problem with the lectotype designation has been brought to my notice. In the caption to fig. 57 I mistakenly referred to the illustrated specimen (NMING:F6030) as being the 'lectotype' rather than being a 'paralectotype'. I have been advised that in doing so it appears that two specimens were 'designated' as lectotype. This invalidates my intended designation of a valid lectotype for the species. It is the purpose of this note to rectify this mistake, to designate a valid lectotype for *Rhombocladia dichotoma* (M'Coy, 1844), to illustrate it, and to list the valid paralectotypes.

Order **FENESTRATA** Elias & Condra, 1957

Suborder **PHYLLOPORININA** Lavrentjeva, 1979

Family **CHAINODICTYONIDAE** Nickles and Bassler, 1900

Genus **RHOMBOCLADIA** Rogers, 1900

TYPE SPECIES. *Rhombocladia delicatula* Rogers, 1900, by original designation; from the Upper Carboniferous of Kansas, U.S.A.

Rhombocladia dichotoma (M'Coy, 1844)

Fig. 1

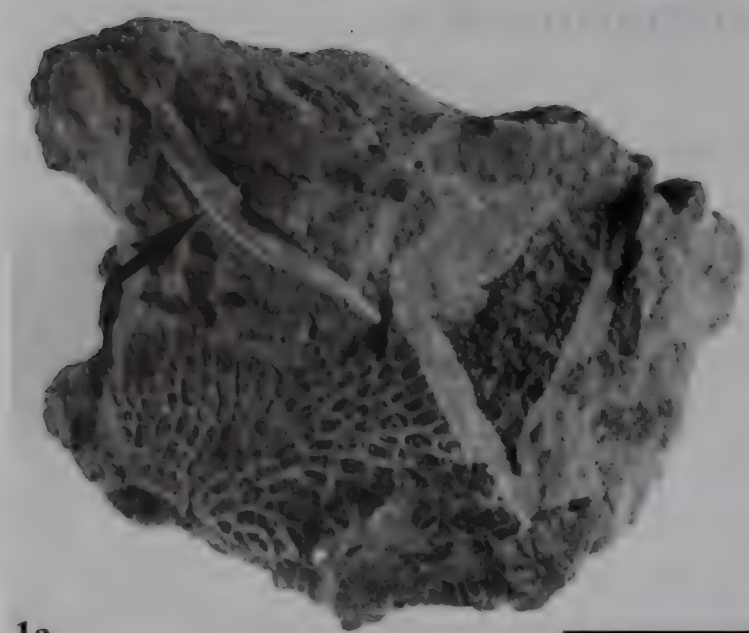
LECTOTYPE. Herein designated: NMING:F7058; Black Lion, near Enniskillen, County Cavan (Viséan, Asbian); Griffith Collection.

PARALECTOTYPES. NMING:F6030; no locality given (?Viséan); Griffith Collection; figured M'Coy 1844: pl. 27, fig. 15 and Wyse Jackson 1996: fig. 57. NMING:F7056–F7057, F7059–F7060; Black Lion, near Enniskillen, County Cavan (Viséan, Asbian); Griffith Collection. NMING:F7061; Millicent, Clane, County Kildare (Viséan, Chadian); Griffith Collection. NMING:F7486–F7489; Kildare, County Kildare (Viséan); Griffith Collection. Sedgwick Museum, Cambridge, SMC:E5188; Howth, County Dublin (Courceyan/Chadian, Dinantian); Griffith Collection. SMC:E5189/a–b; Killymeal, Dungannon, County Tyrone (Viséan, Brigantian); Griffith Collection. SMC:E5190; Kildare, County Kildare (Viséan); Griffith Collection.

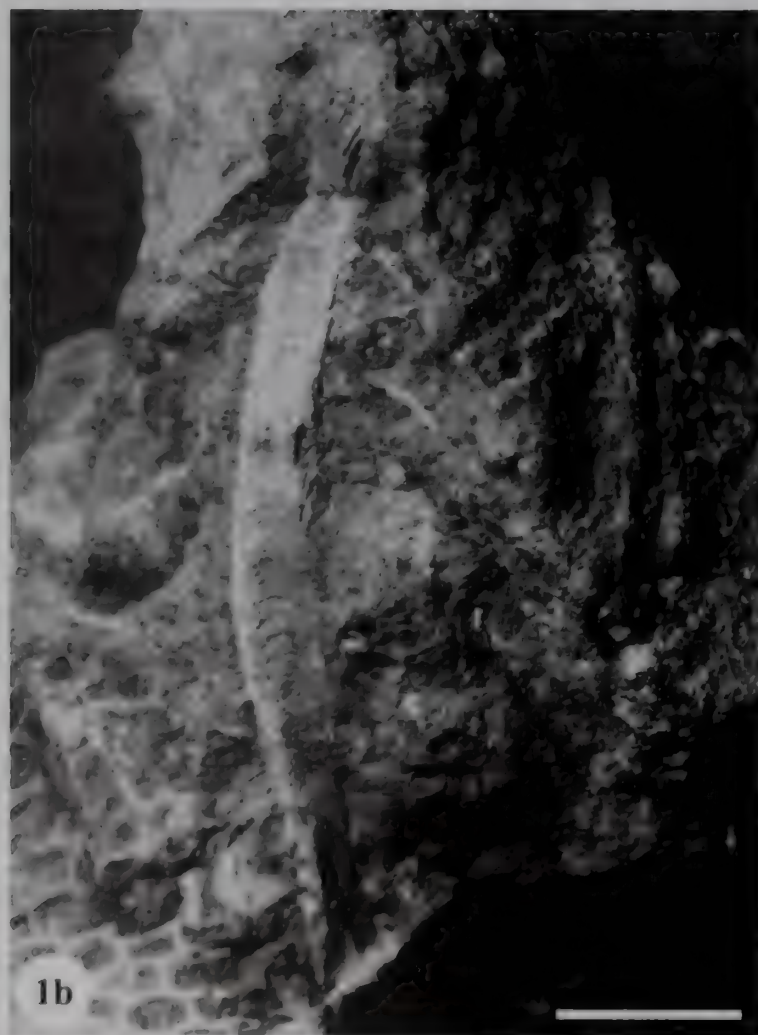
ACKNOWLEDGEMENTS. I am grateful to Nigel Monaghan (National Museum of Ireland) for alerting me to this problem, and for the advice of Dr Philip Tubbs (International Commission on Zoological Nomenclature).

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Wyse Jackson, P.N. 1996. Bryozoa from the Lower Carboniferous of County Fermanagh, Ireland. *Bulletin of the Natural History Museum, Geology Series*, **52** (2): 119–171.



1a



1b

Fig. 1 *Rhombocladia dichotoma* (M'Coy, 1844). NMING:F7058 (lectotype); Black Lion, near Enniskillen, County Cavan (Viséan, Asbian); Griffith Collection. **1a**, general view of lectotype (arrowed), $\times 2$. Scale bar = 10 mm. **1b**, detail of 1a, showing reverse surface with semi-circular growth lines, $\times 5$. Scale bar = 4 mm.

The Gough's Cave human fossils: an introduction

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SYNOPSIS. Locality details, lists of collections and details of age dating are given for specimens recovered from Gough's Cave, Cheddar, Somerset, as an introduction to 16 papers describing this hominid and other mammal material, that are due to be published in this and succeeding issues of the *Bulletin*.

Gough's (New) Cave in Cheddar Gorge, Somerset (Fig. 1), has been known as an archaeological and palaeontological site for over a century (Jacobi 1985; 1991; this series). It has produced a wealth of late Pleistocene (Oxygen Isotope Stage 2) fauna and Upper Palaeolithic (sometimes termed 'Creswellian') artefacts, mainly through incidental discoveries made during its continuing development as a show cave (Fig. 2). Through large numbers of direct radiocarbon dates on faunal material (see e.g. Housley 1991) it is known that most of these finds derive from the 'Lateglacial Interstadial', approximately 11,500–13,000 radiocarbon years ago (= approximately 13,000–14,500 calendar years: see Fig. 3), and although the Pleistocene human material will be treated as a single assemblage here, it is possible that the Lateglacial human occupation covered a wider range than this would imply (Hedges *et al.* 1991). The Lateglacial fauna consists of species such as *Equus ferus*, *Cervus elaphus*, *Bos primigenius*, *Saiga tatarica*, *Lepus timidus*, and (from worked, possibly imported, examples) *Mammuthus primigenius* (Currant 1986, 1991; this series; Lister 1991), and much of this faunal material shows evidence of human butchery or modification (Currant 1991; this series; Andrews & Fernández-Jalvo this series). The site has also produced terminal Pleistocene and early and late Holocene material.

Gough's Cave has also produced a large, but disparate, sample of fossil human material, beginning with the discovery of the first elements of the 'Cheddar Man' skeleton in 1903. This skeleton, here termed Gough's Cave 1 (as in Oakley *et al.* 1971), has been directly dated as early Holocene (inferred Mesolithic) in age, and it remains the most complete ancient human skeleton known from the British Isles. Over the succeeding 90 years, numerous additional finds of human skeletal material have been made at the site, culminating in the extensive Lateglacial material excavated between 1986–1992 (the localities are shown in Figs 2, 4). This latter material was almost all excavated from about a cubic metre of fine gravel and silty sediments wedged between a large rock and an overhang from the north wall in area I (Figs 2, 4; Currant *et al.* 1989; Macphail & Goldberg, this series), lying immediately above the previously recorded conglomerate extending into the 'Cheddar Man fissure'. Short reviews of these finds have been published (Stringer 1985; Currant *et al.* 1989; Stringer 1990; Cook 1991) and they are summarised in Table 1. It is evident from the present studies that the following minimum numbers of individuals are represented by human skeletal or dental material:

Late Holocene. Three individuals: one child (3–8 years); one adolescent (12–14 years); one older adult.

Early Holocene/Mesolithic. One individual ('Cheddar Man'): young adult.

Late Pleistocene/Creswellian. Five individuals: one child (approximately 3 years at death); two adolescents/young adults; one young/mid-adult; one older adult.

In this and succeeding issues of the *Bulletin*, the Gough's Cave Late Pleistocene (Creswellian) and early Holocene (Gough's Cave 1 – 'Cheddar Man') human material will be described and analysed in papers by different workers, and the Creswellian assemblages will be subjected to taphonomic analyses. There will also be papers on the associated sedimentology, archaeology and mammalian faunas of Gough's Cave. The planned publications are listed below. Three of them (papers 2–4) describe both Pleistocene (Creswellian) and Holocene material (including Gough's Cave 1), while the others specifically describe either Late Pleistocene (Creswellian) material or Gough's Cave 1.

1. Taphonomy of the Creswellian (Pleistocene) faunal and human remains from Gough's Cave (Somerset, England): a case of cannibalism? P. Andrews & Y. Fernández-Jalvo.
2. The human cranial remains from Gough's Cave (Somerset, England). L. Humphrey & C. Stringer.
3. The human mandibles from Gough's Cave (Somerset, England). A. Rosas & C. Stringer.
4. The human dental remains from Gough's Cave (Somerset, England). D. Hawkey.
5. The Creswellian (Pleistocene) human upper limb remains from Gough's Cave (Somerset, England). S. Churchill.
6. The Creswellian (Pleistocene) human axial skeletal remains from Gough's Cave (Somerset, England). S. Churchill.
7. The Creswellian (Pleistocene) human lower limb remains from Gough's Cave (Somerset, England). E. Trinkaus.
8. Gough's Cave 1 (Somerset, England): a study of the pectoral girdle and upper limbs. S. Churchill.
9. Gough's Cave 1 (Somerset, England): a study of the hand bones. E. Trinkaus.
10. Gough's Cave 1 (Somerset, England): a study of the axial skeleton. S. Churchill & T. Holliday.
11. Gough's Cave 1 (Somerset, England): a study of the pelvis & lower limbs. E. Trinkaus.
12. Gough's Cave 1 (Somerset, England): an assessment of sex and age at death. E. Trinkaus, L. Humphrey, C. Stringer, S. Churchill & R. Tague.
13. Gough's Cave 1 (Somerset, England): an assessment of body size and shape. T. Holliday & S. Churchill.
14. Gough's Cave, Cheddar, Somerset: microstratigraphy of the Late Pleistocene/earliest Holocene sediments. R. Macphail & P. Goldberg.

Table 1 The main human skeletal material from Gough's cave, Cheddar. Data from Stringer (1985, 1990), and further radiocarbon dates from Hedges *et al.* (1991). As discussed in Hedges *et al.* (1991), the discrepancy in the radiocarbon dates for Gough's Cave 2 may be due to contamination from post-excavation treatment of the 1927–28 finds.

SPECIMEN	DATE FOUND	ACTUAL OR INFERRED LOCATION OR STRAT POSITION	AGE	DETAILS	ORIGINAL DESCRIPTION
GC1 'Cheddar Man'	1903/1935	'Cheddar Man fissure' spit 9?	Early Holocene/Mesolithic. 9080±150 BP (tibia: BM-525); 9100±100 BP (talus: OxA-814)	Partial skeleton adult male	Seligman & Parsons 1914
GC2	1927-28	Spit 12-13	Late Pleistocene/Creswellian. 11480±90 BP (OxA-2234); 11820±120 BP (1987 frontal conjoin: OxA-2795)	?Adult calotte	Keith & Cooper 1929 (called 'skull 1', suggested adult male)
GC3	1927-29	Spits 10-11, 14	Late Pleistocene/Creswellian. 11990±90 BP (OxA-2235)	Child calvaria	Keith & Cooper 1929 (called 'skull 2', suggested 3-year old female)
GC4	1927-28	Spit 7	Late Holocene	Adol. Cranial and maxilla	Keith & Cooper 1929
GC5	1927-28	Spit 7	Late Holocene	Adult maxilla	Keith & Cooper 1929
GC6	1928-29	Spit 14	Late Pleistocene/Creswellian. 11700±100 BP (OxA-2236)	Adult mandible	Cooper, in Parry 1931
GC7	1950	Spit 14	Late Pleistocene/Creswellian	Suggested right parietal fragment, but may be left	Tratman 1975
No number	1927-28	Spits 6-7	? Late Holocene	Postcranial frags, now lost	
No number	1928-29	Spit 16	Late Pleistocene/Creswellian	Humerus, now lost	
No number	1949-51	Spits 12, 14	Late Pleistocene/Creswellian	Postcranial fragments	Papers in this series
I.1/38	1959	Spit 15+	Late Pleistocene/Creswellian	Left scapula	Stringer 1985
M.23.1/1	1959	Spit 15+	Late Pleistocene/Creswellian	Left clavicle	Stringer 1985
M.23.1/2	1959	Spit 15+	Late Pleistocene/Creswellian. 12300±100 BP (OxA-2796)	Right scapula	Stringer 1985
Marked '7'	Unknown	Unknown	?Late Pleistocene/Creswellian	Left scapula	Stringer 1985
Finds no. 22 and 87	1986-7	Area I (See figure 2)	Late Pleistocene/Creswellian	Adolescent maxillae	Papers in this series
Find no. 49	1986-7	Area I	Late Pleistocene/Creswellian	Adolescent mandible, same individual as maxillae	Papers in this series
Find no. 139	1987	Area I	Late Pleistocene/Creswellian	Adult maxillae	Papers in this series
Find no. 190	1987	Area I	Late Pleistocene/Creswellian. 12380±110 BP (OxA-2796)	?Adult calotte	Papers in this series
Find no. 253	1987	Area I	Late Pleistocene/Creswellian	Adult right hemimandible	Papers in this series
Additional finds	1986-1992	Area I	Late Pleistocene/Creswellian	Numerous dental, cranial and postcranial frags	Papers in this series

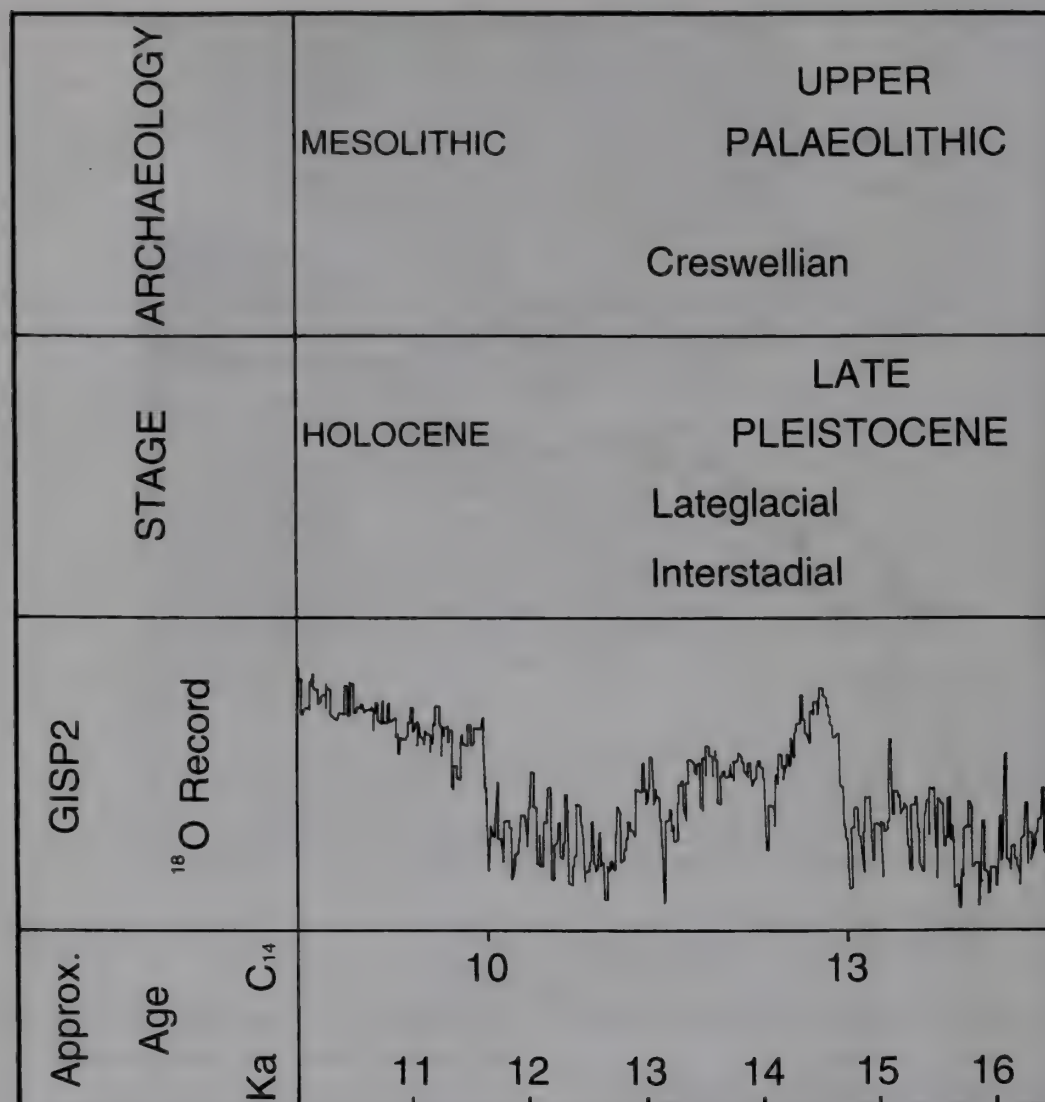


Fig. 3 Time scale, climatic record, stratigraphic, and archaeological divisions for the Late Pleistocene – early Holocene.

important roles in the excavation and post-excavation work. Throughout the excavations we were made most welcome by the staff of the Cheddar Caves, particularly Sandra Lee and Chris Bradshaw, and subsequently, Hugh Cornwell and Bob Smart. We are also grateful to Lord Weymouth for his permission to carry out the excavations, and for his subsequent approval of the transfer of the Gough's fossil human material to The Natural History Museum. Preparation, conservation and replication of the Gough's Cave material were carried out by members of the Palaeontology Conservation Unit and much of the photography by the Photographic Unit of The Natural History Museum. Figures 1–3 were produced by Phil Rye.

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Fig. 4 Area I excavation at Gough's Cave (1986–1992). Area I is lower left in this photograph, the 'Cheddar Man fissure' centre right.

The Creswellian (Pleistocene) human axial skeletal remains from Gough's Cave (Somerset, England)

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SYNOPSIS. Human axial skeletal elements are described from Pleistocene deposits in Gough's Cave. They include 10 vertebrae and 51 rib fragments belonging to at least three individuals, possibly one male and two females. Some of the ribs show marks made by stone tools, suggesting human damage before they were deposited.

INTRODUCTION

Axial skeletal elements from the Pleistocene deposits of Gough's Cave include 10 vertebral and 51 rib fragments. Some of the vertebrae and ribs are nearly complete, but most are broken and incomplete. A number of ribs also bear cut marks attributable to stone tools (see Andrews & Fernandez-Jalvo, *in litt.*), suggesting some degree of human induced damage and breakage prior to deposition.

The axial remains represent at least three individuals. A number of the preserved vertebrae articulate well, and it is possible that all of the vertebrae recovered derive from a single individual (although one specimen is slightly smaller than the others and may represent a second individual). However, based on the size and morphology of the ribs, most of them derive either from a smaller, possibly female, individual and a larger, possibly male, individual. Six rib fragments, representing ribs from the middle of the series of the left side, appear to represent a third individual. The corresponding ribs in the other two individuals are relatively well represented, so it is unlikely that these six fragments belong to the other two series. The ribs of this third individual are more similar in size and thickness to those of the smaller, more complete individual, and thus they may represent an additional female. Five humeral fragments were recovered from these deposits, a right side humerus from a larger individual and two right and two left side fragments representing smaller individuals, making it probable that the axial remains also sample at least three individuals (note, however, that the overall representation of upper limb remains suggests at least four individuals are represented in the sample).

The vertebral fragments are described first, followed by treatment of the rib remains grouped by individual. Specimens are referred to by their current Natural History Museum designations (M.54###), followed by excavation numbers in parentheses. Comparative vertebral dimensions were drawn from the literature, while for the ribs, comparative data are limited to a small sample of recent European-Americans ($n = 20$, Franciscus & Churchill, *in press*).

VERTEBRAL REMAINS

Inventory

M.54042 (GC 87 134)

This is a largely complete second cervical vertebra (axis) (Fig. 1). There is some damage to the dorsal part of the spinus process and to

the lateral aspects of the transverse processes bilaterally (however, both transverse foramina are intact). Damage to the lateral side includes a part of the right side inferior articular facet (roughly one-half of the facet is preserved). Cut marks abound on the ventral surface from the base of the articular facet on the dens to the inferior edge of the body.

The bone is from a large adult (all secondary centers of ossification are fused and the epiphyseal lines are obliterated). The facets for articulation with the first cervical vertebra are large (with a maximum diameter anterolaterally to posteromedially of 16.2mm). There is some rugosity on the inferior surface of the neural arch at the junction of the right and left laminae, probably representing the attachment of the median thickening of the bands of the ligamentum flavum. Although there is a slight extension of the left side inferior annular ring that may reflect some incipient exostotic growth, there are no clear signs of degenerative changes on any of the articulating surfaces. This specimen articulates well with M.54043.

M.54043 (GC 87 174 & CG 87 226D)

These two fragments conjoin to form a portion of a typical cervical vertebra (Fig. 2). The specimen preserves the corpus and the right side pedicle, inferior and superior articular facets, lamina (almost to midline), and part of the transverse process (lacking the anterior and posterior tubercles and the costotransverse bar – *i.e.*, the anterolateral side of the foramen). There is some damage to the anterior surface of the body. The body is small with well developed uncinate processes superiorly. Based on the preserved portion of the right side lamina, the vertebral foramen was roughly as long anteroposteriorly as it was wide mediolaterally. The pedicle is relatively short, and the superior articular facet is directed superoposteriorly. These features suggest that this element belongs to the superior portion of the cervical series (excluding vertebrae C1 and C2). This specimen articulates well with M.54042 (a second cervical) superiorly and with M.54044 inferiorly (Fig. 3), suggesting that this is a third cervical vertebra and that these three vertebrae represent the same individual.

The pedicles, judging from the preserved right side, were fully fused at the time of death.

M.54044 (GC 87 177)

This is a corpus of a cervical vertebra, with some slight damage to the anterior surface (Fig. 4). The body is slightly larger than that of M.54043 and makes an excellent fit with its inferior surface, and this is most likely to be the subjacent vertebra (C4).

The uncinate processes are well developed. The pedicles are broken away from the centrum and there are no traces of epiphyseal

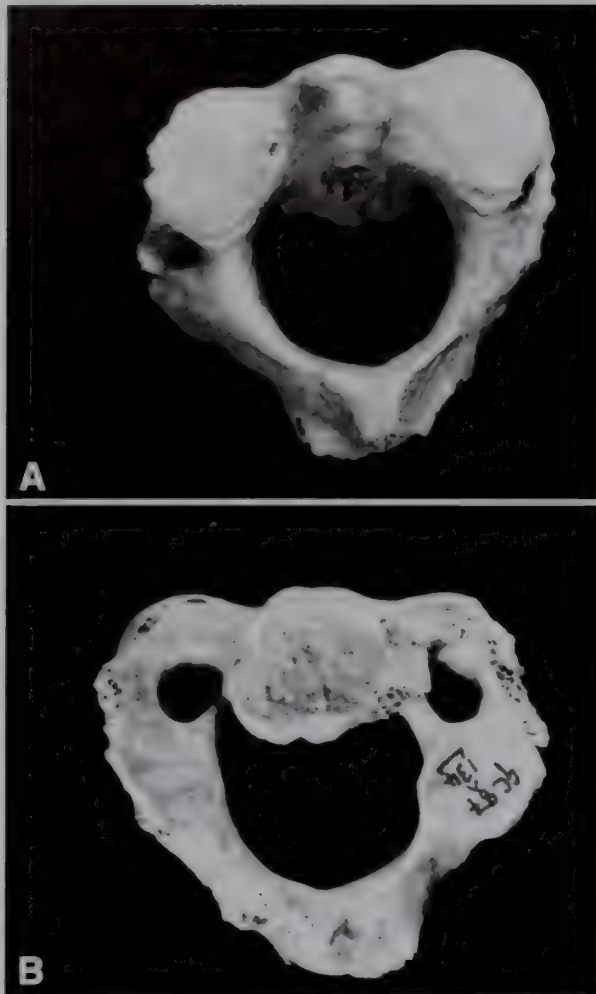


Fig. 1 Second cervical vertebra, M.54042. **1a**, superior; **1b**, inferior; $\times 1$.

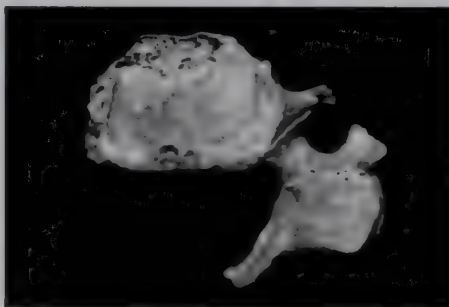


Fig. 2 Cervical vertebra, M.54043, superior, $\times 1$.

surfaces, suggesting that the pedicles were fully fused at the time of death.

M.54045 (GC 87 122 B)

This is a fragment of the left side superior and inferior articular facets of a cervical vertebra, including a small portion of the lamina and pedicle (Fig. 5). The transverse foramen is broken away. Based on the size and orientation of the articular facets this fragment appears to be from a cervical vertebra fairly low in the sequence (C5 or C6). The size of the lamina, pedicle and articular facets is consistent with the size of the other cervical vertebrae described here, thus this fragment probably belongs to the same individual.

M.54046 (GC 87 226 B)

This fragment preserves the body and right side pedicle, superior and inferior facets, and partial lamina of a cervical vertebra (Fig. 6). The costotransverse bars are broken away bilaterally, and the preserved



Fig. 3 Cervical vertebrae M.54042 (above), M.54043 (middle) and M.54044 (below) in articulation. Lateral, $\times 1$.

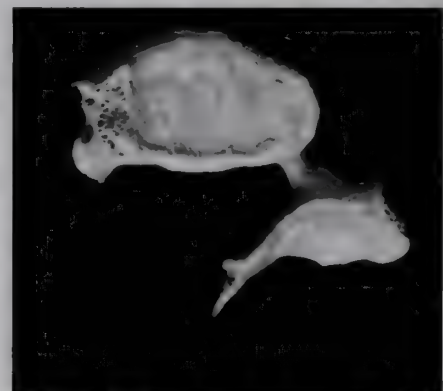


Fig. 4 Cervical vertebra, M.54044, superior, $\times 1$.

right side transverse process lacks the posterior tubercle. Again the overall size is consistent with the other cervical vertebrae recovered and this element probably represents the same individual. The corpus is relatively wide mediolaterally, and the vertebral foramen was clearly wider mediolaterally than it was long anteroposteriorly. These features clearly indicate that the element is from the lower part of the cervical series. This specimen has a relatively flat inferior border to the body, suggesting that it is a C7 (vertebra prominens).

The preserved right side uncinate process (the left side process is damaged) is large and projecting. The superior articular facet faces posteriorly, superiorly and slightly medially. There is no evidence of degenerative changes on any of the adjoining surfaces. The preserved pedicle is fully fused to the centrum.

M.54047 (GC 87 152)

This is a fragment of a right side neural arch from a thoracic vertebra (Fig. 7). The fragment preserves the pedicle and most of the costal

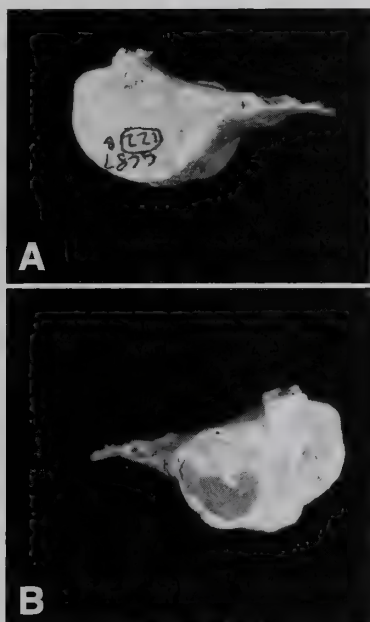


Fig. 5 Left side articular facets of cervical vertebra, M.54045. **5a**, superior; **5b**, inferior; $\times 1$.

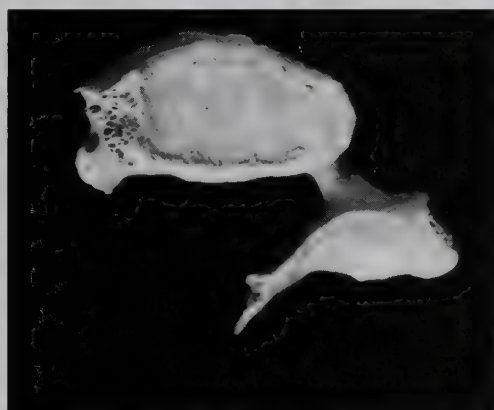


Fig. 6 Cervical vertebra, M.54046, superior, $\times 1$.

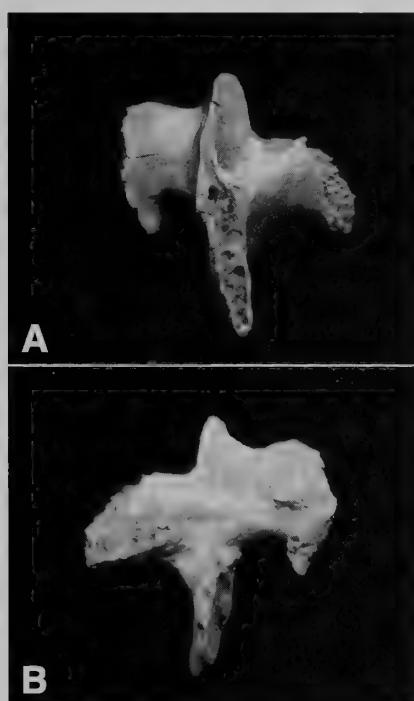


Fig. 7 Thoracic vertebral fragment, M.54047. **7a**, medial; **7b**, lateral; $\times 1$.

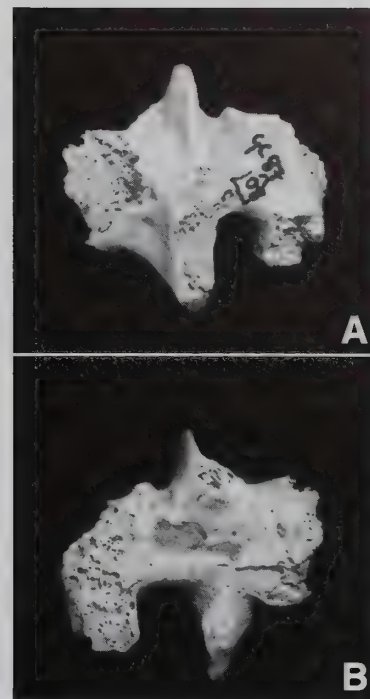


Fig. 8 Thoracic vertebral fragment, M.54048. **8a**, lateral; **8b**, medial; $\times 1$.

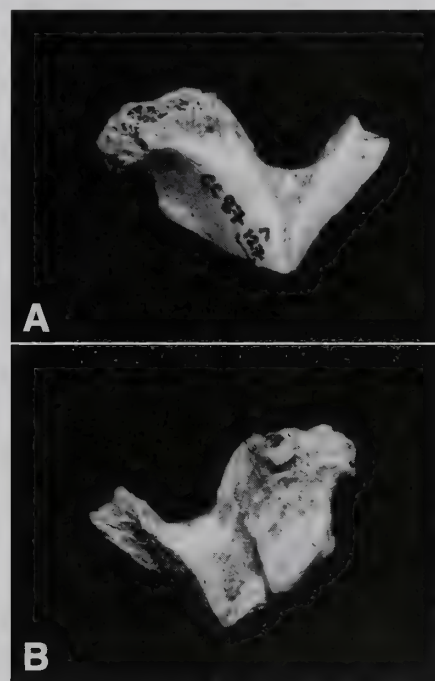


Fig. 9 Thoracic vertebral fragment, M.54049. **9a**, superior; **9b**, inferior; $\times 1$.

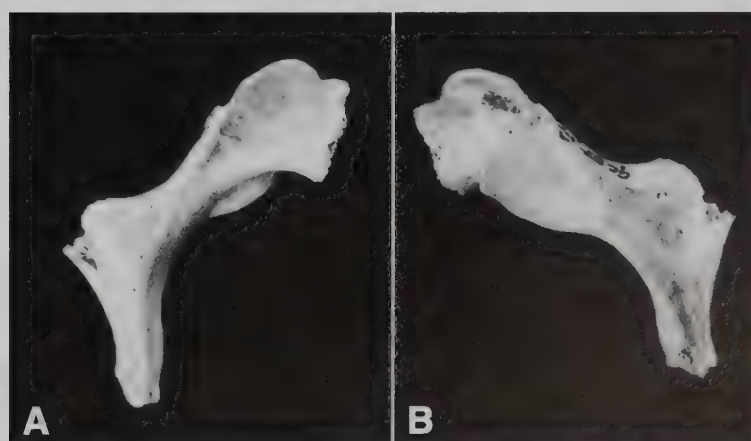


Fig. 10 Thoracic vertebral fragment, M.54050. **10a**, superior; **10b**, inferior; $\times 1$.

Table 1 Dimensions (mm) of the cervical vertebrae.

	M.54042 (C2)	M.54043 (C3)	M.54044 (C4)	M.54046 (C7)
Superior external transverse articular diameter ¹	45.4	—	—	—
Superior internal transverse articular diameter ²	19.1	—	—	—
Superior transverse articular diameter ³	32.3	—	—	—
Inferior internal transverse articular diameter ⁴	20.9	—	—	—
Inferior transverse articular diameter ⁵	(32.2)	—	—	—
Spinal canal dorso-ventral diameter (M-10)	22.9	—	—	—
Spinal canal transverse diameter (M-11)	24.2	—	(22.9)	—
Body ventral height (M-1)	22.3	(11.0)	13.5	13.2
Body dorsal height (M-2)	16.6	12.3	12.8	12.6
Body median height (M-3)	—	11.7	11.7	11.0
Odontoid process height (C2) (M-1a)	14.0	—	—	—
Body superior dorso-ventral diameter (M-4) ⁶	11.7	(13.4)	13.5	14.5
Body superior transverse diameter (M-7)	—	17.4	18.6	(26.4)
Body inferior dorso-ventral diameter (M-5)	16.4	15.8	14.7	15.8
Body inferior transverse diameter (M-6)	18.6	19.4	20.2	25.9

1. Maximum distance between the lateral edges of the superior articular facets.

2. Maximum distance between the medial edges of the superior articular facets.

3. Average of the external and internal transverse articular diameters of the superior articular facets.

4. Maximum distance between the medial edges of the inferior articular facets.

5. Distance between the (estimated) midpoints of the inferior articular facets.

6. For the C2, measurement was taken in the transverse plane defined by the medial edges of the superior articular facets.

Table 2 Dimensions (mm) of the second cervical vertebrae.

Specimen	VBH ¹	SCTD ¹	SCDVD ¹	OPH ¹	Reference
Gough's Cave Creswellian	22.3	24.2	22.9	14.0	
Chancelade 1 (♂)	(26) ²	—	—	13	Billy, 1969
Predmost 3 (♂)	19.0	25.5	18.0	12.0	Matiegka, 1938
Predmost 4 (♀)	16.5	22.4	18.0	10.8	Matiegka, 1938
Predmost 9 (♂)	—	22.0	15.0	12.5	Matiegka, 1938
Predmost 14 (♂)	19.5	24.6	16.5	13.3	Matiegka, 1938
Skhul V (♂)	18.0	26.0	24.6	12.5	McCown & Keith, 1939; Stewart, 1962
Fossil mean ³	19.8	24.1	18.4	12.4	
SD, (n)	3.7 (5)	1.8 (5)	3.7 (5)	0.9 (6)	
European-American males (n = ±96) ⁴	—	24.1	17.1	—	Lanier, 1939
African-American males (n = ±88) ⁴	—	23.9	16.2	—	Lanier, 1939

1. VBH = ventral body height (M-1); SCTD = spinal canal transverse diameter (M-11); SCDVD = spinal canal dorsoventral diameter (M-10); OPH = odontoid process height (M-1a).

2. Taken as [total anterior height] - [odontoid process height] from reported values.

3. Mean of fossils (sexes combined) excluding the Gough's Cave Creswellian material.

4. Mean value, no standard deviation reported.

facet of the body, the superior and inferior articular processes, a very small bit of the lamina, and a portion of the transverse process (none of the costal facet of the transverse process is present) with a very small portion of the inferior tubercle. Judging from the small size of the articular facets, the fragment probably comes from a thoracic vertebrae fairly high in the sequence (T1–5). The articular facet on the body looks large relative to the pedicle (larger than the demi-facets usually seen on thoracic vertebrae), so this fragment may represent the first thoracic vertebra. However, the superior articular facet makes a poor fit with the inferior facet of the possible seventh cervical vertebra M.54046 (which may not, however, represent the same individual).

This specimen has a large cutmark across the base of the transverse process, but based on coloration it looks to have been recently imposed, possibly during excavation or preparation. The right side pedicle is fully fused with the centrum, suggesting that this bone derived from an adult.

M.54048 (GC 87 108 C [1014.0])

This is a small fragment representing a portion of the right side dorsolateral body of a thoracic vertebra, with the right pedicle,

superior and inferior articular facets, and a small bit of the transverse process and lamina (Fig. 8). A small portion of the superior surface of the vertebra is preserved. The demi-facet for the rib head is not preserved, but that this bone represents a thoracic vertebra is clear given the size of the pedicle and the orientations of the articular processes (Bass, 1987). In thoracic vertebrae, the position of the superior demi-facets on the corpi migrates dorsally going from T1 to T12 (personal observation). Generally by the middle of the thoracic series the demi-facet is partially or wholly on the pedicle. There is no sign of the demi-facet on the lateral surface of the pedicle in this specimen, and this, combined with the overall morphology of the articular process, suggests it is from the higher part of the sequence (likely T1–T5). The right side pedicle is fully fused to the body.

M.54049 (GC 87 127)

This is a neural arch fragment from a thoracic vertebra, preserving most of the left lamina, including the inferior articular facet and the base of the transverse tubercle, and a small portion of the right lamina (Fig. 9). The neural arch is small relative to the other vertebrae recovered, and may represent another, perhaps subadult or female, individual.

Table 3 Anterior and posterior body heights (mm) of cervical vertebrae.

Specimen		C3	C4	C5	C6	C7	Reference
Gough's Cave Creswellian	ant	(11.0)	13.5	—	—	13.2	
	post	12.3	12.8	—	—	12.6	
Gough's Cave 1 (Cheddar Man) (♂)	ant	—	—	—	(12.2)	—	
Chancelade 1 (♂)	ant	12	—	12.5	13	13	Billy, 1969
	post	14.5	—	15.5	15	15	
Oberkassel 2 (♀)	ant	12	—	—	—	—	Billy, 1969
	post	13	—	—	—	—	
Arene Candide 2 (♂)	ant	11	11	12	12	14	Paoli <i>et al.</i> , 1980
	post	13	14	13	13	15	
Arene Candide 3 (♀)	ant	—	—	—	12	14	Paoli <i>et al.</i> , 1980
	post	—	—	—	14	14	
Arene Candide 10 (♂)	ant	—	—	—	—	(13)	Paoli <i>et al.</i> , 1980
	post	—	—	—	—	(13)	
Arene Candide 12 (♂)	ant	—	10	—	12	—	Paoli <i>et al.</i> , 1980
	post	—	12	—	12	—	
Abri Pataud (♀)	ant	12.5	—	—	—	—	Billy, 1969
	post	13	—	—	—	—	
Predmostí 3 (♂)	ant	11.3	(12)	12.0	11.0	13.0	Matiegka, 1938
	post	12.6	12.7	14.0	13.4	14.5	
Predmostí 9 (♂)	ant	—	—	12.4	11.6	13.0	Matiegka, 1938
	post	—	12.8	13.0	14.0	14.0	
Predmostí 14 (♂)	ant	13.0	12.2	12.0	11.8	—	Matiegka, 1938
	post	13.0	13.0	15.0	15.5	16.0	
Skhul V (♂)	ant	—	8.5	9.5	(10)	—	McCown & Keith, 1939; Stewart, 1962
	post	10.5	9.5	10.5	(13)	(12.5)	
Fossil males ¹ , mean SD, (n)	ant	11.8	10.7	11.7	11.7	13.2	
		0.9 (4)	1.5 (5)	1.1 (6)	0.9 (8)	0.4 (5)	
	post	12.7	12.3	13.5	13.7	14.3	
		1.4(5)	1.5(6)	1.8(6)	1.2 (7)	1.2 (7)	
Fossil females ¹ , mean SD, (n)	ant	12.3	—	—	12	13	
		0.4(2)	—	—	(1)	(1)	
	post	13.0	—	—	14	13	
		0.0 (2)	—	—	(1)	(1)	
European-American males (n = ±96) ²	ant	14.1	13.5	12.7	12.7	14.4	Lanier, 1939
	post	14.0	13.7	13.7	13.6	15.0	
African-American males (n = ±88) ²	ant	13.3	12.8	12.1	11.9	13.8	Lanier, 1939
	post	13.4	12.8	12.6	12.7	14.0	

1. Fossil mean, excluding the Gough's Cave Creswellian material.

2. Mean value, no standard deviation reported.

M.54050 (GC 87 127 A)

This is a fragment of neural arch of a thoracic vertebra. The fragment preserves the right lamina, including the superior and inferior facets and the base of the transverse process, and most of the spine (Fig. 10). It is clearly from a larger individual than that represented by M.54049.

The superior facet rounds down onto the superior surface of the root of the transverse process. The inferior facet rounds dorsally along its inferior margin, producing an inferiorly facing 'lip' on the facet. Based on the shape of the facets and overall morphology of the fragment, this appears to represent a vertebra from somewhere in the middle of the thoracic column.

Morphology

The fragmentary nature of the vertebrae from the late Pleistocene deposits at Gough's Cave make it difficult to reach any conclusions about their morphology. Of the ten vertebral fragments recovered, nine may represent the same individual. The tenth, M.54049, appears to derive from a smaller, perhaps female or subadult (although the two lamina of the neural arch are fully fused together) individual. Because of the fragmentary state of these remains, few osteometric observations could be made (Table 1).

Comparative data taken from the literature is provided in Tables 2

and 3. The comparative samples of European Upper Paleolithic fossils are admittedly small, especially with respect to female specimens. In terms of cervical vertebral body heights, M.54043, tentatively attributed to a C3, is small in both ventral and dorsal body heights relative to males and females of comparable geological age (Table 3). However, M.54044, attributed to a C4, has body heights higher than the small sample of Upper Paleolithic males presented in Table 3. M.54046, a possible C7, has a ventral body height equal to the mean value of five Upper Paleolithic males (and very close to the dimension obtained for a single female), but has a dorsal body height more than one standard deviation below the Upper Paleolithic male mean (but very close to the value obtained for the single female) (Table 3). In all the cervical vertebrae in which body heights could be determined, the dimensions from the Gough's Cave sample are smaller than the mean values obtained by Lanier (1939) on a sample of ± 96 European-American skeletons. While it is not possible to make reasonable inferences about the sex of the individual represented by these remains, it is possible to conclude that this individual was small by Paleolithic and modern standards. This is also reflected in dimensions of the spinal canals and the odontoid processes of the C2 (Table 2). Given that a single fragment, M.54049, may represent an individual who was smaller still, this sample seems to represent a relatively small body-sized population.

COSTAL REMAINS

Introduction

As noted above, most of the ribs from the Pleistocene deposits of Gough's Cave can be confidently attributed to one of two individuals. Six rib fragments (representing three ribs) that do not appear to fit with the other two individuals (on the basis of curvature and posterior angle morphology) indicate the presence of a third individual.

The first individual was the smaller, and had lightly constructed ribs (Fig. 11; Table 4). These ribs tend to have proximal bodies that are square or rectangular in section with wide, inferiorly directed subcostal grooves (generally extending proximally to the tubercle). The subcostal grooves are formed by the flat inferior surface of the rib internally and a crest for *M. iliocostalis* and/or the external intercostal muscle externally. The reassociation of most of the ribs of this individual was based on similarities in 1) size, 2) curvature, and 3) the morphology of the *M. iliocostalis* line (the *M. iliocostalis* line is superoinferiorly compressed in this individual and runs almost horizontally (proximodistally) along the rib). The right-side eleventh rib was attributed to this individual based on its curvature (it is too curved to fit with the ribs of the second individual) and small size. The right and left twelfth ribs were attributed to this individual based on the similarity in superoinferior diameter between them and the right eleventh rib. The heads of all but one rib are missing from this individual, raising the possibility that they were unfused (the smaller size and gracility of these ribs would fit with their deriving from a subadult individual). However, the proximal surfaces are all either covered in matrix or too damaged to evaluate the state of fusion of the heads. The one rib preserving the articular surface of the head (the right 11th rib, M.54014) retains a portion of the actual articular surface. In this rib the head appears to be fused, but the epiphyseal line may not be entirely obliterated. Other possibilities for the lack of

recovery of the vertebral ends of the ribs include breakage at the time of disarticulation from the vertebrae, or post-mortem damage. However, eight of the ten identifiable ribs preserve a substantial amount of the neck proximal of the tubercle, and three preserve the base of the head, so it seems unlikely that post-mortem damage would so uniformly damage the heads but not the necks. Thus it seems likely that the heads were not fused to the costae in this individual.

The second individual is larger and more robust (Table 5; Fig. 12). The ribs are thick mediolaterally and are more heavily muscle marked. The proximal shafts tend to be more rounded in section, and the subcostal groove tends to be more internally directed and, in a number of the ribs, does not extend proximally much beyond the posterior angle. Reassociation of the ribs of this individual was based on similarities in 1) size and curvature, 2) mediolateral thickness of the corpi, 3) *M. iliocostalis* line morphology (the line is more vertically oriented in this individual, and the ribs are superoinferiorly broader at the posterior angle so that the *M. iliocostalis* attachment area does not form a 'tubercle' as it does in the first individual), and 4) subcostal groove morphology. The ribs tend to be broken proximally between the posterior angle and the tubercle. Of fifteen fragments clearly attributable to this individual, only two preserve the tubercle (one of these being a proximal fragment that also preserves the head), and an additional one has a tiny portion of the tubercle preserved. The single fragment preserving the head shows a fully fused articular surface, indicating that this individual was likely greater than 20 years old at death (Williams & Warwick, 1980). The ribs of this individual tend to be more heavily cutmarked than those of the smaller individual.

Three ribs do not seem to fit, on the basis of size, curvature and *M. iliocostalis* line morphology, with these other two individuals. These are all left side ribs, and two of them are very similar in morphology and appear to be adjacent ribs (Fig. 13). The third is thicker mediolaterally, but matches the other two in overall curvature. This larger, thicker rib may represent one of the lower typical ribs, so the difference in mediolateral thickness might reflect variation along the series (or perhaps the rib belongs to yet another individual). For the time being these three ribs will be considered as a third individual.

Individual ribs were identified as to side and number using overall size and shape, the position of the *M. iliocostalis* line, and the size and shape of the articular facets. Sequencing the ribs was facilitated by comparisons of the fossil specimens to sequenced ribs from recent human skeletons from the collections of the Natural History Museum. Sequencing of the complete series from the modern comparative skeletons was based on criteria outlined in Dudar (1993), Jellema *et al.* (1993), Mann (1993), and Franciscus & Churchill (in press). After identifying each fossil rib based on its diagnostic morphological features and comparison with the sequenced recent human series, the two sets of fossil ribs were sorted on the basis of size and morphology, and then laid out in sequence. This allowed for the refinement of earlier assessments by comparing aspects of *M. iliocostalis* placement, the relative height of the rib heads in the sagittal plane (Mann, 1993), and size and curvature from rib to rib.

Metric observations of the ribs are recorded in Tables 6–9.

Table 4 Ribs attributed to Individual 1.

Rib	Left	Right
1	M.54001	—
2	M.54002	M.54009
3	M.54003	—
4	M.54004	M.54010
5	M.54005	M.54011
6	M.54006	M.54012
7–9	M.54007	M.54013
11	—	M.54014
12	M.54008	M.54015

Table 5 Ribs attributed to Individual 2.

Rib	Left	Right
1	M.54016	—
2	M.54017	M.54026
3	M.54018	M.54027
4	M.54019	M.54028
5	M.54020	M.54029
6	M.54021	M.54030
7	M.54022	—
6–9 (right)	—	M.54031
8–9 (left)	M.54023	—
	M.54024	—
	M.54025	—
10	—	M.54032

INVENTORY

Individual 1

RIB 1

Left: M.54001 (GC 87 56)

The left first rib is represented by a single fragment (Fig. 11). The fragment lacks only the head and portions of the sternal end, and is



Fig. 11 Ribs of individual 1, superior, $\times 0.5$.

also missing a piece of bone roughly 25mm in length along the distal external edge. The straight line distance from the ventral-most margin of the articular tubercle to the ventral-most point of the sternal end of the rib (McCown & Keith, 1939: fig. 75) is roughly 72mm, while the maximum subtense from this line to the lateral-most extent of the rib shaft (*ibid.*) is ca. 25mm. Abundant cutmarks can be seen on the superior surface in the region of the proximal attachment area for *M. scalenus medius* (the cutmarks extend along the internal edge from the neck to the level of the distal tubercle). Cutmarks can also be seen on the superior proximal and distal sides of the tubercle, which may reflect cutting of the lateral costotransverse ligament. There is some slight weathering to the distal superior surface of the shaft.

The ligamentous part of the tuberosity is neither rugose nor large. The crest for *M. scalenus medius* along the superior proximal surface of the shaft is insignificant and non-rugose. There is a small crest on the external edge of the rib distal of the tubercle that may represent the lateral limit of this muscle. There are no other visible muscle markings on the bone. There is no perceptible scalene tubercle, so the grooves for the subclavian artery/1st thoracic nerve and subclavian vein run together into one shallow, poorly delimited sulcus.

RIB 2

Right: M.54009 (GC 87 220)

Left: M.54002 (GC 87 132)

Both second ribs are represented by fragments. The right second rib

preserves a part of the head, the tubercle and the proximal shaft up to but not including the attachment area for *M. serratus posterior superior* (and extending further on the internal side). The total length of this fragment is 62.3mm. Most of the head is missing or eroded. The partial preservation of the head allows for a rough estimate of neck length (the distance from the middle of the head to the middle of the articular tubercle) of ca. 24mm. Cutmarks are visible on the neck (especially on the inferior neck surface) and on the nonarticular tubercle. The left 2nd rib is represented by a proximal fragment. The rib is completely preserved from the neck to the proximal end of the *M. scalenus posterior* crest, after which only the internal edge is preserved for another 42mm. The total length of the fragment is 70.4mm.

The articular facets are relatively large for a second rib (measuring 9.8mm proximodistally by 7.8mm superolateral-inferomedial on the right; 9.5mm PD by 7.7mm SL-IM on the left). The nonarticular tubercles do not present themselves as single tubercles immediately adjacent to the articular facets, but instead as a series of two or three rugose ridges running superoproximally to inferodistally. On the left-side rib, the nonarticular tubercle extends along the external inferior margin as a crest for the attachment of the intercostal muscles and membranes.

The proximal end of the *M. serratus posterior superior* tuberosity is visible on the superior lateral surface of the right-side rib. The left-side preserves the proximal and distal portions of the *M. scalenus*

Table 6 Dimensions (mm) of the ribs of Individual One.

Rib	Prox. thick. ¹	Prox. height ²	Shaft thick ³	Shaft height ⁴
LI	16.2	3.9	—	—
RII	12.6	6.6	—	—
LII	12.6	6.1	—	—
LIII	6.5	9.4	5.7	10.0
LIV	7.9	7.5	8.0	8.9
LV	8.2	(8.1)	10.6	6.1
RVI	8.0	9.9	10.9	(11.7)
LVI	—	—	10.9	9.1
RXI	4.7 ⁵	8.7 ⁵	5.4	11.2

1. Proximal thickness (internal-external diameter of rib body just distal of the tubercle) [M-2].

2. Proximal height (superoinferior diameter of rib body just distal of the tubercle) [M-1].

3. Shaft thickness (internal-external diameter of rib body at posterior angle).

4. Shaft height (superoinferior diameter of rib body at posterior angle).

5. Taken just distal of head.

posterior crest. This crest appears to have been very large, with a deep adjacent intercostal sulcus. At the proximal extent of the crest, the body of the rib has a superoinferior diameter of 8.2mm, and the sulcus is 4.1mm deep. The distal end of the crest can be seen on the preserved portion of the internal edge fragment. This provides a minimum proximodistal length of 34.7mm for the *M. scalenus posterior* attachment. The *M. levator costae* insertion areas are preserved bilaterally and are only mildly rugose. The preserved attachment areas for the intercostal muscles and membranes on the interior edges of the superior surfaces are moderately rugose.

RIB 3

Left: M.54003 (GC 87 213)

Only the left third rib is preserved (Fig. 11). This rib is represented by a fragment 100.4mm in total length, complete from just distal of the head proximally to somewhere near mid-shaft distally.

The articular facet measures 8.8mm proximodistally by 6.4mm superoinferiorly. The rib has a very marked *Mm. intercostales* sulcus on its superior margin, formed in part by a relatively large *M. serratus anterior* crest on the superolateral surface of the rib. The rib also has a weakly developed non-articular tubercle, and a subcostal sulcus that is very large and extends proximally past the articular tubercle.

Torsion in the body of the rib (such that a cross-section of the body at mid-shaft would have its long axis running from superointernal to inferoexternal), as well as other aspects of overall morphology, is consistent with this being a third rib.

RIB 4

Right: M.54010 (GC 87 148 & 114B & 114C)

Left: M.54004 (GC 87 94)

The fourth ribs are both present (Fig. 11). The right rib was reconstructed from three fragments. The rejoined fragments produce a proximal rib fragment about 167mm in total length, preserving a portion of the neck proximally, the articular and non-articular tubercles, and the body to around midshaft. The left fourth rib is represented by a proximal fragment with a total length of 111.3mm. The articular surfaces of the head are missing, but the rest of the head, neck and articular and nonarticular tubercle are complete. The preserved portion of the head allows for a very rough estimate (since the articular surfaces are missing) of neck length (see above) of ca. 22mm. The shaft is complete internally to about midshaft. The external surface is complete to about 35mm distal of the posterior angle, after which trabeculae are exposed. A few cutmarks can be seen on the internal surface of the neck of the right side rib.

The superior edge of the neck of the left rib continues distally as

a very weak crest for the superior costotransverse ligament. This crest becomes distinct at its merger with the attachment of the *M. intercostales externi* and the *M. iliocostalis* line. In the left rib, the *Mm. intercostales* form a distinct yet shallow sulcus along the superior edge. The articular facets are relatively small, measuring 9.9mm (proximodistally) by 8.1mm (mediolaterally) on the right and 9.7mm (PD) by 8.1mm (ML) on the left, and are very slightly curved. On the right side, the shallow subcostal groove begins at the articular facet. On the inferior edge of the left side rib the subcostal groove is very poorly developed and is hardly discernible. In this rib there is a very small flange where the *M. iliocostalis* line crosses the inferior margin.

RIB 5

Right: M.54011 (GC 87 265 & 89 013)

Left: M.54005 (GC 87 34 & 48)

The right fifth rib has been reconstructed from two fragments. Together they comprise the proximal half of the rib, preserved from just proximal of the articular tubercle to somewhere below midshaft distally (Fig. 11). Much of the rib body is covered in matrix, and distally the internal and external surfaces have split apart and filled with matrix. The exposed surfaces are slightly weathered. The total length of the rejoined fragment is ca. 194mm. The left fifth rib was reconstructed from three fragments (two bearing the same field designation, GC 87 48). This is a virtually complete rib, about 167mm in length. Proximally the head is missing its articular surface, and distally a small bit of the sternal end is lacking. A very rough estimate of neck length (see above) of ca. 24mm can be obtained from the preserved portions. Although the specimen is missing a small portion of the sternal end, it is possible to estimate the straight line distance from the ventral-most rim of the articular tubercle to the ventral-most point of the body (McCown & Keith, 1939: fig. 75) at 177mm, and the maximum subtense from that line to the external-most point on the shaft (*ibid.*) as 58mm. The bone has adherent matrix and small rocks, and the exposed surfaces are weathered. Large cutmarks are visible on the sternal end of the left side rib.

As in the fourth ribs, the articular tubercles are relatively small (9.5mm proximodistally by 8.0mm mediolaterally on both sides). The non-articular tubercles are not very pronounced. In the left rib, the superior edge of the neck continues distally as a raised crest for the superior costotransverse ligament and the *M. levator costae*. This ridge passes laterally of the proximal attachment area of the *Mm. intercostales*, the two ridges together forming a distinct sulcus proximal of the posterior angle. The *M. levator costae* crest continues distally to the angle and merges with the *M. iliocostalis* line. The *M. iliocostalis* scar is relatively small in the left side and is virtually horizontal. The morphology of the *M. iliocostalis* line cannot be determined on the right side rib because of overlain matrix, but the subcostal groove is relatively large and there is a small flange on the inferior rib margin in the region of the iliocostal line. The subcostal grooves are not strongly developed. The ribs are relatively thick, and in the left rib a distinct yet shallow sulcus can be seen on the superior edge marking the attachment of the intercostal muscles.

RIB 6

Right: M.54012 (GC 87 134A)

Left: M.54006 (GC 89 004 & 008)

The right sixth rib is represented by a 64.3mm long fragment, and is preserved from the neck just proximal of the tubercle to the shaft just distal of the posterior angle (Fig. 11). The bone is weathered over its entire surface and has cutmarks on its external surface distal to the posterior angle. The left side rib has been reconstructed from two fragments. The reconstructed rib has a total length of 229mm and is

preserved from the neck to the region of the anterior angle. The proximal end up to and including the articular tubercle is buried in matrix. Most of the external surface is damaged and there is matrix adherent to much of the bone.

In the right rib the articular tubercle is concave proximodistally and is oriented dorsally. It measures 8.3mm (PD) by 8.6mm (SI). The *M. iliocostalis* lines are not well marked. The shafts are rectangular in section, with very mediolaterally broad subcostal grooves.

RIBS 7–9
Right: M.54013 (GC 87 125A)
Left: M.54007 (GC 87 165A)

Two fragments (Fig. 11), one from a right and one from a left side rib, could not be securely identified as to number. Based on size and morphology, they most likely represent ribs in the series seven through nine. By the same criteria, these ribs most likely are associated with the other ribs of Individual One.

The first of these fragments, M.54013, comes from a right rib. The fragment is 99.9mm long and represents the body of a typical rib. The preserved portion derives from somewhere between the posterior and anterior angles. The weathered internal and external surfaces have become separated and infilled with matrix. Besides a portion of the subcostal groove, no landmarks or muscle attachment scars are visible. The preserved portion of subcostal groove is narrow superoinferiorly (ca. 2.5mm SI), and the ‘roof’ is at an angle of ca. 120°–130° to the internal surface.

The second fragment, M.54007, is 49.7mm long and derives from the mid-distal end of a left typical rib. What appears to be a line for the external oblique muscle, marking the anterior angle, is visible on the external surface. The fragment has a mediolateral diameter of 5.2mm and superoinferior diameter of 12.8mm at the anterior angle.

RIB 11
Right: M.54014 (GC 87 207)

Only the right side eleventh rib is preserved (Fig. 11). This is a virtually complete rib, missing only some sections of the distal shaft external surface. The sternal end is missing, but based on the tapering of the corpus it appears that the bone is broken very close to the distal end. The total length of the fragment is 121.8mm. The overall preservation of the element is very good, and several cutmarks are visible on the external surface of the neck and on the distal external surface.

Only a portion of the proximal articular surface is preserved. The secondary center of ossification appears to be fused to the neck, but it is not clear if the epiphyseal line was closed. There is no articular nor non-articular tubercle, and only a slight development of the subcostal groove. There are very clearly marked and moderately rugose attachment areas for the *Mm. intercostales* on the inferior (a 22.5mm long scar at about midshaft) and superior (a much longer rugose sulcus from midshaft running distally) edges.

RIB 12
Right: M.54015 (GC 87 257)
Left: M.54008 (GC 87 21)

Both twelfth ribs are preserved (Fig. 11). The right side rib is represented by a fragment with a length of 51.6mm. The fragment is preserved from somewhere proximal of midshaft to the area of the anterior angle (preserving a portion of the shaft where it tapers distally). The bone is slightly weathered on its superior external surface. The left twelfth rib is represented by a 75.9mm fragment preserving most of the distal end, from around mid-shaft proximally to just proximal of the distal tip (the distal end is slightly eroded, but the tapering end that marks this as a 12th rib is clearly evident).

In the right side rib, there is a slight rugosity in the area of the *M.*

intercostale externi attachment, and there is a pronounced tubercle at the *M. serratus posterior inferior* insertion. The left rib exhibits a sulcus for *M. intercostale interni* on the superior margin of the intercostal surface. This rib also shows rugose but small crests that form small sulci on the inferior margin, marking the attachment of *M. erector spinae* (on the external surface) and *M. quadratus lumborum* (on the internal surface). Although their attachment areas are preserved, the left rib does not have visible attachment areas for the diaphragm or *Mm. latissimus dorsi* and *externus obliquus*. Both ribs display small, roughened ‘tubercles’ marking the *M. serratus posterior inferior* insertions along the inferior margins at the anterior angles.

The right side rib is somewhat smaller than its antimere. At the anterior angle, the right rib has a superoinferior diameter of 10.2mm and a mediolateral diameter of 4.2mm, while the left has an SI diameter of 12.7mm and an ML diameter of 4.5mm. However, the two are similar in the morphology of the *M. serratus posterior inferior* insertion scars (it is uncommon to see any visible rugosity in this region in recent human twelfth ribs, thus the similar development of this muscle in both ribs supports their identification as antimeres).

Individual 2

RIB 1
Left: M.54016 (GC 87 217)

Only the left first rib is preserved (Fig. 12). The fragment is 45.1mm long and has a mediolateral width of 21.0mm. The fragment preserves portions of the superior and inferior surfaces and the convex external edge. The superior margin is relatively smooth and preserves the distal portion of the *M. scalenus medius* tubercle. Numerous cutmarks can be observed on the superior surface along the external edge.

RIB 2
Right: M.54026 (GC 86 212)
Left: M.54017 (GC 86 26)

Fragments of both second ribs were recovered (Fig. 12). M.54026 is a section of a right second rib, preserved from the region of the posterior angle proximally to just ventral of the *M. scalenus posterior* crest distally. The fragment has a maximum anteroposterior length of 65.2mm. The fragment preserves all surfaces, but more of the internal margin of the bone is preserved than is the external margin. M.54017 is a fragment of a left 2nd rib, very similar in preservation to its antimere. The left rib is preserved from the region of the posterior angle proximally to a few centimeters distal of

Table 7 Dimensions (mm) of the ribs of Individual Two.

Rib	Prox. thick. ¹	Prox. height ²	Shaft thick ³	Shaft height ⁴
RII	(14.4)	(7.1)	–	–
LII	13.7	7.1	–	–
RIII	–	–	9.4	13.9
LIII	8.3	9.6	9.3	12.0
RIV	8.4	9.3	10.2	13.9
LIV	–	–	8.0	14.6
RV	–	–	10.3	15.7
LV	9.7	(9.8)	10.1	(17.2)
LVI	8.4	9.0	8.7	18.8
LVII	8.2	9.9	8.3	18.2
RVI–IX	–	(11.5)	–	–
LIX?	8.1	10.5	–	–
RX	–	–	7.7	15.6

1–4. See notes in Table 6

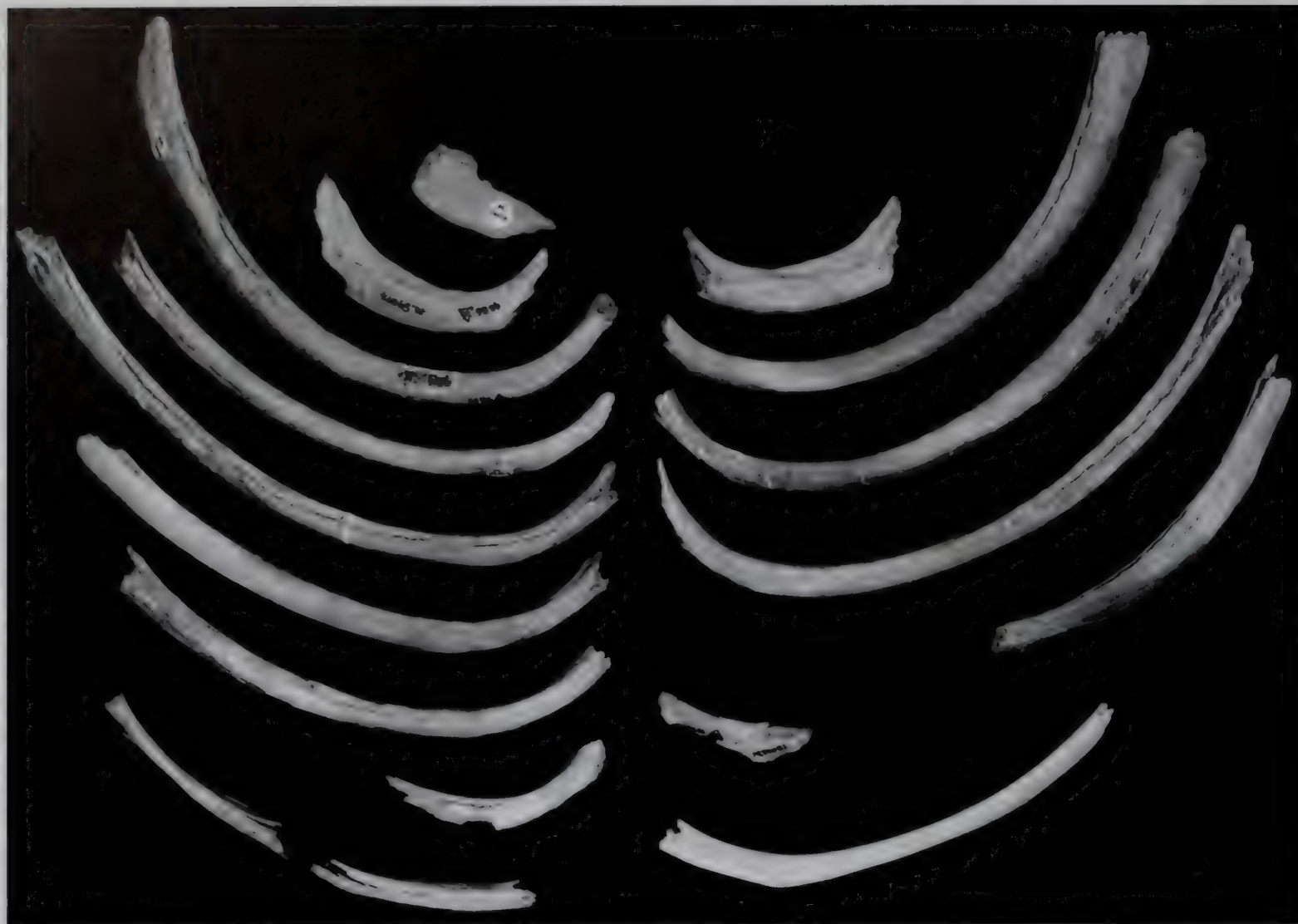


Fig. 12 Ribs of individual 2, superior, $\times 0.45$.

M. scalenus posterior crest distally. The maximum length of the fragment is 73.5mm.

Both ribs are stout with well defined muscle markings. The strength of these ribs is illustrated by their mediolateral diameters at the distal-most point on the *M. scalenus posterior* crest, which measure 17.2mm and 17.5mm in the right and left sides, respectively. The *M. scalenus posterior* crests are very clear and prominent in both ribs, with deep sulci medially for the attachment of the intercostal muscles and membranes. At their points of maximum development the *M. scalenus posterior* crests project 3.3mm in the right rib and 3.2mm in the left (taken as the difference between the superoinferior diameters of the rib on the muscle crest and in the adjacent sulcus). Given that this muscle often leaves no discernible crest in recent human second ribs, this indicates marked muscularity of the upper thorax of this individual. These crest are 34.6mm (right) and 27.6mm (left) in length proximodistally. In the right rib, there is some rugosity visible in the area of the *M. levator costae* attachment, but none in the area of the *M. serratus posterior superior* attachment. On the left side rib, neither of these muscles left discernible scars. In both ribs there are distinct crests on the inferior proximolateral surface marking the proximal extent of the attachment of the *Mm. intercostales*. This crest is most likely just distal of the non-articular tubercle, the position at which proximal thickness and height are taken. Mild rugosity extends distally along the attachment area of the intercostal muscles and pleura.

RIB 3

Right: M.54027 (GC 86 8)

Left: M.54018 (GC 86 12)

The right third rib preserves most of the body (Fig. 12). This 167.5mm long fragment is intact from the posterior angle proximally to somewhere proximal of the anterior angle distally. The proximal break line on the external surface follows the *M. iliocostalis* line. There is some very slight weathering to the external surface of the shaft distal of the posterior angle, but otherwise the bone is well preserved. Some very fine cutmarks can be seen on the exterior surface of the shaft about 39mm distal of the intersection of the *M. iliocostalis* line with the inferior margin of the shaft. The right third rib has a slight irregularity to its distal shaft, perhaps representing a healed fracture. Most of the body of the left third rib is preserved, from the non-articular tubercle proximally (none of the articular facet is preserved) to somewhere proximal of the anterior angle (Fig. 12). None of the sternal chondral articular surface is preserved. Matrix still adheres to the broken proximal end. The total length of the specimen is 207.8mm. Scratch marks (perhaps cutmarks) are visible on the external surface of the shaft.

The *M. levator costae* attachments are visible in both ribs, although more of this region is preserved in the left rib. In the right side a portion of a small and very slight crest can be seen, while the left rib retains a distinct and rugose crest for the insertion of *M. levator costae* and the proximal intercostal muscles. What is preserved of the

M. iliocostalis line in the right rib is a clear but non-rugose scar. In the left rib, the *M. iliocostalis* scar is well defined, with distinct proximal and distal crests. The ribs are relatively thick mediolaterally with distinct, albeit shallow *Mm. intercostales* grooves along the superior edges. The ribs show some asymmetry in the development of the subcostal grooves. On the right side the subcostal sulcus is very poorly developed and cannot even be seen for most of the length of the specimen. In the left, the subcostal groove is large and well marked in the region of the posterior angle, with a well developed crest along the exterior surface of the inferior border.

RIB 4

Right: M.54028 (GC 86 7)

Left: M.54019 (GC 87 181)

The right fourth rib preserves most of the corpus (Fig. 12). The specimen has a total length of 182.0mm, and is complete from the very distal end of the tubercle proximally to somewhere proximal of the anterior angle. The shaft has some very slight weathering damage as well as a few small bits of adherent matrix distal of midshaft but otherwise is well preserved. Cutmarks can be seen on the superior margin of the external surface of the body proximal to mid-shaft. Most of the body of the left fourth rib is represented. The total length of this fragment is 158.3mm, and the bone is preserved proximally from just distal of the non-articular tubercle to somewhere proximal of the anterior angle distally. The specimen is badly weathered and partially eroded along its inferior half. Very fine cutmarks can be made out in two locations on the external surface near the distal break.

In both ribs, the *M. iliocostalis* lines and *M. levator costae* insertion areas are clearly evident, but are not rugose. The *M. iliocostalis* lines terminate as small inferiorly projecting flanges at their intersections with the inferior margins of both ribs. The subcostal sulci are wide and shallow, and both ribs are relatively thick mediolaterally.

RIB 5

Right: M.54029 (GC 87 163)

Left: M.54020 (GC 87 160)

Both fifth ribs are preserved (Fig. 12). The right fifth rib preserves most of the body. The fragment is 191.7mm long and is complete from the body between the tubercle and posterior angle proximally (the internal surface extends farther than the external and may include a portion of the shaft deep to the tubercle, and perhaps even part of the neck) to somewhere proximal of the anterior angle (again the internal surface extends farther and may end just at the anterior angle). The shaft has some weathering damage just distal of the posterior angle but is otherwise well preserved. Cutmarks can be seen on the superior margin of the external surface of the body at or just distal to mid-shaft. The left fifth rib is similarly represented. This rib fragment has a total length of 197.3mm and is preserved from the very distal-most point on the non-articular tubercle proximally to somewhere proximal of the anterior angle distally. The rib shows some slight weathering on its external surface and has a few spots of crushing, but overall is well preserved.

The left rib displays a moderate ridge in the region of the *M. levator costae* insertion. In both sides the *M. iliocostalis* lines are clearly marked but not rugose. In the right rib there is a large flange at the posterior angle where the *M. iliocostalis* line intersects the inferior border (this region is damaged in the left side rib). The bodies of both ribs are mediolaterally expanded and both sides have superoinferiorly wide subcostal grooves (in the region of midshaft, the right-side rib subcostal sulcus has an SI diameter of 4.6mm).

RIB 6

Left: M.54021 (GC 87 45)

Only the left sixth rib could be securely identified (Fig. 12). Two right side rib fragments (described below) could not be confidently identified as to number, and one or both of these may represent the right side sixth rib.

M.54021 preserves the body of left sixth rib, from just distal of the tubercle to below midshaft (but proximal of the anterior angle). The total length of this relatively well preserved specimen is 163.8mm.

The *M. iliocostalis* line begins as a tubercle on the superior edge of the rib, then runs obliquely to the posterior angle. The line is not very marked and is difficult to discern.

RIB 7

Left: M.54022 (GC 86 22)

Only the left seventh rib could be securely identified (Fig. 12). Two right side rib fragments (described below) could not be confidently identified as to number, and one or both of these may represent the right side seventh rib.

The left seventh rib is represented by a fragment that preserves the body from just distal of the tubercle to below midshaft (but proximal of the anterior angle). The total length of the fragment is 146.5mm. Cutmarks can be seen on the superior edge of the external surface near the middle of the preserved portion.

The scar for the *M. levator costae* is clearly defined and moderately rugose. The *M. iliocostalis* line is difficult to distinguish, but its point of intersection with the inferior edge of the rib is clear. The superoinferior diameter of the body proximal of the subcostal groove is small (10.4mm), but by the midshaft region the subcostal groove is large, giving the body a superoinferior diameter of 18.1mm.

INDETERMINATE RIBS 6–9

Right: M.54031 (GC 86 14)

M.54030 (GC 86 'Mr. Barrett's find' Skeleton Pit)

Left: M.54023 (GC 87 134)

M.54024 (GC 87 130)

M.54025 (GC 87 31)

M.54031 preserves the head, neck and tubercle of a right side typical rib. The total length of the fragment is 46.9mm. Damage to the proximal end obliterates the crest of the head, but it is clear that two articular facets were present. A neck length (see above) of ca. 29mm can be estimated from the preserved morphology. In posterior view, the articular tubercle can be seen to be directed inferiorly and the non-articular tubercle is positioned directly distally (on the inferior part of the external surface and rounding down on the inferior edge). The rib body has a superoinferior diameter (proximal height [M-1], Martin, 1928) of 11.5mm just distal of the tubercle.

An additional specimen, M.54030, is a 121.8mm long fragment of the anterior body of a right typical rib. This specimen appears to preserve the anterior angle. The distal end of the superior groove for the *M. intercostales* can be seen on the proximal end of the fragment. There is no subcostal groove in this element (even though the inferior edge of the rib is preserved), and no sternal chondral articular surface is preserved. The rib is large and the proximal end is mediolaterally thick.

A third fragment, M.54023, represents the mid-proximal portion of a left typical rib. The fragment is 65.7mm long and preserves the non-articular tubercle and most of the articular tubercle proximally, and is complete distally to the beginning of the posterior angle on the external surface and to just distal of the posterior angle on the internal surface. The shaft between the tubercle and angle is mediolaterally thick. The articular facet is preserved distally, is relatively flat, and is 8.0mm wide at its widest point (with a length > 9.5mm). The flat articular surface is consistent with a rib from the

series 7–9 (McMinn & Hutchings, 1985). What may be incipient marginal lipping is evident on the superodistal edge of the articular tubercle. There is a distinct sulcus between the articular and non-articular tubercles. Rugosity is visible on the superior surface in the area of the *Mm. intercostales* and *levator costae* attachment sites. The inferior margin has pronounced rugosities in the region of the insertion of the intercostal muscles, just distal of the tubercle. The proximal end of the subcostal groove is present, but the groove is damaged further distally. There is an oblique crest (running superoproximal to inferodistal) on the external surface of the shaft 11.3mm distal of the non-articular tubercle (taken from the crest at the shaft superoinferior mid-point to the middle of the tubercle). This may represent a lateral extension of fibres from the *M. levator costae longus*, indicating that this represents a ninth rib.

A fourth fragment, M.54024, preserves 65.9mm of the body of a rib. The side is indeterminate. The external surface is damaged but preserves some scratches (perhaps cutmarks) on the external surface. Based on size and thickness, this fragment is likely to be from a typical rib belonging to Individual Two.

A fifth fragment, M.54025, preserves 71.9mm of rib body. The side is indeterminate. There is no indication of a subcostal groove, and therefore the fragment probably represents the anterior portion of one of the main ribs. The external surface bears a very slight rugosity which may represent the attachment area of the external oblique muscle at the anterior angle. In the region of the anterior angle, the rib body has a mediolateral diameter of 5.1mm and a superoinferior diameter of 16.1. Again based on size and thickness, this fragment is most probably associated with Individual Two.

RIB 10

Right: M.54032 (GC 87 147)

Only the right tenth rib is preserved (Fig. 12). This fragment includes 139.6mm of the body of the rib, from just distal of the non-articular tubercle proximally to somewhere between midshaft and the anterior angle distally. The entire surface is slightly weathered. What appear to be cutmarks can be seen on the external surface at the *M. iliocostalis* line.

The *M. iliocostalis* line in this rib is not rugose and is hardly visible (which may be a function of weathering). The insertion of the *M. levator costae* is clearly marked by a small tubercle and associated sulcus. A small tubercle on the inferior edge near the proximal break marks the insertion of the costotransverse ligament.

Individual 3

INDETERMINATE RIBS 4–9

Left: M.54033 (GC 89 021)

M.54034 (GC 87 24 & 10)

M.54035 (GC 87 268 & 180A & 61)

A third individual is represented by three left side ribs (Fig. 13). The first of these is M.54033, a 121.3mm long fragment of the body of a typical rib. The fragment is broken distal to the tubercle proximally and in the vicinity of midshaft distally. Based on the morphology of the body (torsion of the corpus and development of the subcostal groove) this appears to represent a rib from fairly high in the series.

Table 8 Dimensions (mm) of the ribs of Individual Three.

Rib	Prox. thick. ¹	Prox. height ²	Shaft thick ³	Shaft height ⁴
LIV?	(7.4) ⁵	(9.4) ⁵	8.9	–
LV?	7.8	8.5	7.8	14.4

1–4. See notes in Table 6

5. Position estimated

Two fragments conjoin to form most of a left typical rib, M.54034. The total length of the complete rib is 163.5mm. The rib lacks only the articular surfaces of the head proximally, and is complete distally to somewhere proximal of the anterior angle. The entire bone is weathered and there are large cutmarks on the external surface at the distal end. The articular tubercle is relatively large in this specimen (11.5 mediolaterally by 8.0 proximodistally), but the non-articular tubercle is poorly developed. The *M. iliocostalis* line is poorly marked. Again, based on rib morphology this specimen appears to represent a rib from fairly high in the series, and may be the subjacent rib to M.54033.

Three additional fragments conjoin to form a 187.9mm long portion of another left typical rib, M.54035. The reconstructed rib is preserved from the region of the posterior angle proximally to somewhere proximal of the anterior angle. The fragment is uniformly weathered along its length, and the proximal end has some damage to it. The rib is thick mediolaterally (in the midshaft region, the mediolateral diameter of the rib = 9.2mm, the superoinferior diameter = 14.7mm). There is a very slight and moderately rugose sulcus visible on the superior edge for the attachment of the intercostal muscles. The subcostal groove is superoinferiorly broad yet shallow at the proximal end and tapers to nothing at the distal end. Based on the size and morphology of the rib, it is most likely one from the middle part of the series.

Additional rib fragments – unidentifiable as to side, number or individual

Ten rib fragments could not be securely identified as to individual, side (in most cases) or number. The first of these, M.54041 (GC 87 21, but not related to the right side twelfth rib of Individual One that bears the same excavation number), is a 67.2mm long fragment of the internal surface of a rib. A small portion of the superior surface of the subcostal groove is preserved for a length of about 32mm along one edge. Based on overall morphology this appears to be a portion of the body of a typical rib.

M.54036 includes two rib fragments. The first, GC 218A, is a 75.2mm long by 16.7mm high fragment of the external surface of a rib, side indeterminate. No landmarks are visible. The second, GC 218B, is a 51.0mm by 15.5mm fragment of the internal surface of a rib, side indeterminate, and with no visible landmarks. The specimen shows some weathering and surface damage.

M.54037 also includes two fragments, one of which is not a costal fragment. GC 87 134B is a 41.9mm long fragment of subperiosteal bone, likely representing a portion of the external surface of a rib. Some rugosity is evident along one edge, perhaps representing the *M. levator costae* insertion. GC 87 134C is a 62.6mm long fragment of diaphyseal bone. The cortex is 3.3mm thick on one edge and the internal surface is lightly trabeculated with coarse spicules.

M.54038 incorporates three fragments. GC 87 214A is a rib fragment with a total length of 52.1mm and a maximum width of 10.3mm. Only the internal surface is preserved. GC 87 214B is a 30mm long by 11.2mm wide (superoinferiorly) fragment of the external surface of a rib. This fragment also preserves a portion of either the inferior or superior edge. Two series of cutmarks can be seen on this specimen, the first of which are associated with a clean broken edge and likely represent excavation damage, the second consisting of four or more parallel marks, which may also be of recent origin. GC 87 214C measures 24.5mm by 6.5mm, and preserves a portion of the external surface and either the inferior or superior border of a rib.

M.54039 (GC 87 52) is a small fragment of a rib body concreted to a rock. No landmarks are evident on the external surface. The

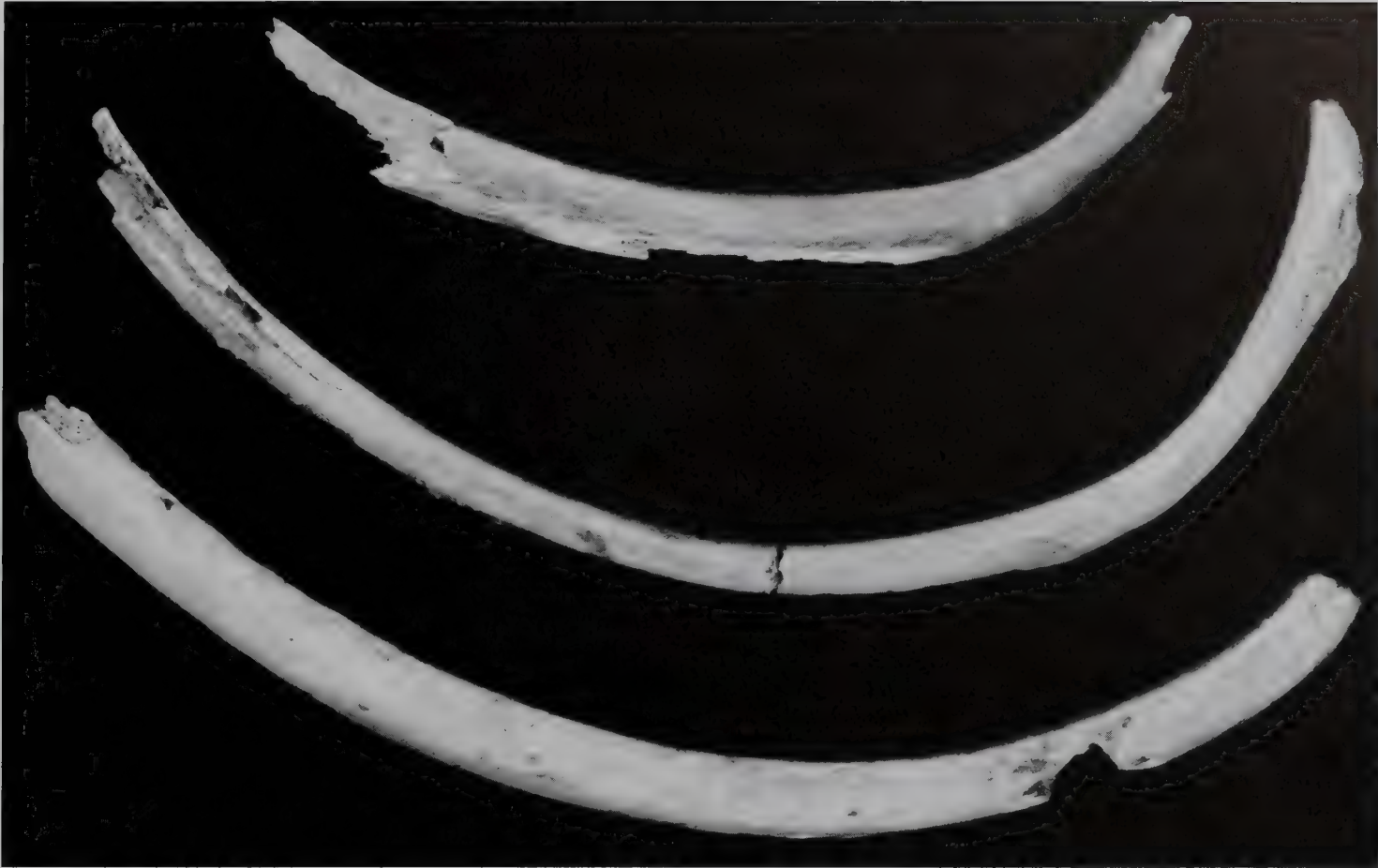


Fig. 13 Ribs of individual 3, superior, $\times 0.9$.

fragment has a maximum length of 28.5mm and a maximum width of 12.7mm. One edge (either superior or inferior margin) is preserved on the side concreted to the rock.

Three small, non-diagnostic rib fragments were given museum designations M.54052 (incorporating two fragments, GC 87 117 A & B) and M.54040 (GC 87 246). In addition, GC 87 208 is the proximal half of a left rib which, because of a strong possibility that it may be non-human, was not given a museum designation. The articular surface of the head of this specimen is unfused and missing. The body below the tubercle is narrow superoinferiorly (7 to 8mm) out to the posterior angle, where the body flares to a superoinferior diameter of ca. 16mm. Just distal of the tubercle, the rib has a mediolateral diameter of 6.3mm and a superoinferior diameter of 7.8mm. The rib bears a round articular tubercle (10mm in diameter) but no non-articular tubercle. A shallow subcostal groove is present. There is no trace of the iliocostalis line at the posterior angle. At the posterior angle, the shaft has a mediolateral diameter of 5.7mm and a superoinferior diameter of 15.3mm. An abrasion (perhaps a cutmark) runs across the external surface distal of the posterior angle. Based on overall morphology (notably the SI flaring of the body distal of the posterior angle), if this rib does derive from a human, it may represent a 10th left side rib.

Morphology

Little can be added to a discussion of the morphology of the ribs to what has already been said above. It is clear that the ribs of Individual 1 derived from a relatively small person. The shaft dimensions of this individual's ribs are generally smaller than those of Individual 2 and the average values of a small sample of Euro-American males (Table 9). Given that vertebral remains described above also derived from a relatively small person, it is possible that they represent the same

Table 9 Rib shaft dimensions in the Gough's Cave Creswellian assemblage and recent European-American males (mean, SD)^a.

Rib	Individ. I	Individ. II	Individ. III	EuroAmericans (n=20)
3	Thickness	5.7 ^b	9.4	7.8 \pm 1.1
	Height	10.0 ^b	13.9	11.2 \pm 1.7
	T/H ratio	0.57 ^b	0.68	0.71 \pm 0.1
4	Thickness	8.0 ^b	10.2	8.6 \pm 0.9
	Height	8.9 ^b	13.9	11.7 \pm 1.9
	T/H ratio	0.90 ^b	0.73	0.74 \pm 0.1
5	Thickness	10.6 ^b	10.3	9.0 \pm 1.0
	Height	6.1 ^b	15.7	12.8 \pm 1.6
	T/H ratio	1.74 ^b	0.66	0.71 \pm 0.1
6	Thickness	10.9	8.7 ^b	9.2 \pm 1.0
	Height	9.1 ^b	18.8 ^b	13.9 \pm 1.5
	T/H ratio	1.20 ^b	0.46 ^b	0.67 \pm 0.1
7	Thickness	—	8.3 ^b	9.0 \pm 1.0
	Height	—	18.2 ^b	15.0 \pm 1.9
	T/H ratio	—	0.46 ^b	0.61 \pm 0.1
10	Thickness	—	7.7	7.1 \pm 1.2
	Height	—	15.6	15.6 \pm 2.3
	T/H ratio	—	0.49	0.46 \pm 0.1
11	Thickness	5.4	—	6.1 \pm 1.0
	Height	11.2	—	12.9 \pm 1.6
	T/H ratio	0.48	—	0.48 \pm 0.1

^a Dimensions for Euro-American males are for right-side ribs and are taken from Franciscus & Churchill, in press.
^b Taken on left-side rib.

individual, likely a female. The ribs of Individual 1 are unusual in their great mediolateral thickness relative to their superoinferior height, at least as indicated by ribs four through six (Table 9). This results in midshaft thickness to height ratios that are between 1.6 and 10.3 standard deviations above the mean ratios in the Euro-American male comparative sample. This extreme mediolateral diameter

of the ribs gives them a rectangular shape in cross-section, and it was in fact this morphology (along with size differences) that allowed for the relatively easy sorting of the ribs of Individuals 1 and 2 (see above).

The second individual is the larger of the three, with rib midshaft dimensions that compare favorably with the mean Euro-American male values in size and shape (Table 9). Based on the comparisons in Table 9, Individual 2 most likely represents a male.

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The Creswellian (Pleistocene) human lower limb remains from Gough's Cave (Somerset, England)

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SYNOPSIS. The Creswellian human remains include a variety of pieces of the lower limbs, all extremely fragmentary and, with the exception of three metatarsals, disassociated. At least four individuals are represented. The remains are notable mainly for their moderately high femoral neck-shaft angles and their pronounced gluteal tuberosities and associated lateral diaphyseal buttresses.

INTRODUCTION

The lower limb remains from the Creswellian levels of Gough's Cave are extremely fragmentary. Except for one fibula and three associated metatarsals, there are no complete diaphyseal contours, and none of the articular surfaces are sufficiently intact to provide more than basic identification and a few qualitative details. Moreover, even though multiple individuals are represented (e.g., there are four left proximal femoral fragments with portions of the gluteal tuberosity, indicating that at least four individuals are present), it is not possible to associate pieces by individual (not including cases in which two pieces actually join along a postmortem break, since they are now catalogued as a single element).

Consequently, the following description provides primarily inventory information, combined whenever possible with morphological observations. Very few standard osteometric dimensions can be determined, or even estimated, on these remains.

In the inventory, the current Natural History Museum catalogue number (M.54####) is provided, followed by an excavation number (or numbers when two or more pieces have been joined).

For some of the remains (e.g., the femora and tibiae) sample sizes are sufficient to divide the remains into smaller and larger morphs. These assessments are based on visual inspection of multiple pieces from the same region of the bone and are not strictly quantified.

PELVIC REMAINS

Inventory

M.54080 (GC 87 114A)

Right

Internal fragment of an iliac blade just anterior of the posterior superior tubercle and just below the iliac crest. Maximum height: 40.5mm, maximum length: 29.0 mm.

M.54090 (GC 87 224A)

Right

Inferior end of the acetabular lunate surface, with the articular surface and the internal edge around the convex end of the subchondral bone adjacent to the acetabular notch. Maximum length: 21.1 mm, maximum breadth: 22.6 mm.

Morphology

These two pieces provide little information, other than that there is no apparent degeneration on the M.54090 subchondral bone.

FEMORA

Inventory

M.54081 (GC 87 85)

Right

Section of the posterior and medial surfaces of a mid femoral diaphysis, with strong development of the linea aspera and a pilaster. Maximum length: 121.9 mm, maximum breadth: 22.4 mm.

M.54085 (GC 87 13)

Right?

Diaphyseal section which probably represents the lateral popliteal surface with the lateral distal crest of a right femur. Maximum length: 107.5mm, maximum breadth: 26.6mm.

M.54115 (GC 1950–51 Level 12)

Right

Medial neck cortical bone with the adjacent trabeculae, from the proximal flare for the head to the mid-posterior flare for the lesser trochanter and the mid-anterior rugosity for the spiral line (Figs 1, 3). Maximum length: 83.0mm.

M.54116 (GC 87 108A)

Right

Medial cortex and trabeculae of the neck, from close to the head to just distal of the lesser trochanter, with most of the medial side of the base for the lesser trochanter (Figs 2, 4). Maximum length: 97.0mm, maximum breadth (antero-posterior): 27.3mm.

M.54117 (GC 49 Level 14)

Left

Proximal lateral diaphysis, with the edge of the greater trochanter and all of the gluteal tuberosity and buttress (Fig. 5). Maximum length: 159.5mm.

M.54118 (GC 86 14A)

Left

Proximal diaphyseal piece with the distal half of the gluteal tuberosity and buttress. Maximum length: 81.8mm, maximum breadth: 19.7mm.



Figs 1, 2 Posterior views of proximal right femora; 1, M.54115; 2, M.54116.

Figs 3, 4 Medial views of proximal right femora; 3, M.54115; 4, M.54116.

Fig. 5 Lateral view of left femur, M.54117.

Fig. 6 Posterior view of right femur, M.54120.

Figs 7-9 Postero-lateral views of femora; 7, M.54123; 8, M.54145; 9, M.54124.

All figures $\times 0.95$

M.54119 (GC 86 14B)

Left

Proximal lateral diaphysis with the middle of the gluteal buttress and tuberosity. Maximum length: 69.6mm, maximum breadth: 23.3mm.

M.54120 (GC 87 138A)

Right

Proximal diaphysis with the distal half to one-third of the gluteal tuberosity and buttress (Fig. 6). Maximum length: 86.5mm, maximum breadth: 20.4mm.

- M.54121 (GC 87 167)
Left
Proximal diaphysis with the distal half of the gluteal buttress and the lateral three-quarters of the gluteal tuberosity. Maximum length: 54.5mm, maximum breadth: 17.9mm.
- M.54122 (GC 1986)
Left
Proximal medial diaphyseal piece, with the spiral line and the beginning of the flare for the lesser trochanter, with medial and antero-medial surface bone. Maximum length: 50.3mm, maximum breadth (antero-posterior): 24.6mm.
- M.54123 (GC 86 17)
Side indeterminate
Midshaft posterior and medial diaphyseal section with the linea aspera (Fig. 7). Maximum length: 49.0mm, maximum breadth: 23.1mm.
- M.54124 (GC 87 200)
Right
Proximal to mid diaphyseal section with the posterior surface and the proximal development of the linea aspera plus the nutrient foramen (Fig. 9). Maximum length: 67.8mm, maximum breadth: 22.6mm.
- M.54125 (GC 87 98/176)
Left
Lateral and especially dorsal sides of an adolescent distal femur, with the metaphyseal surface present especially laterally. Maximum length: 86.0mm, maximum depth: 46.0mm, maximum breadth: 62.7mm.
- M.54145 (GC 87 79)
Side indeterminate
Late juvenile or early adolescent femoral diaphyseal piece (Fig. 8). Maximum length: 60.0mm.

Morphology

Proximal Medial Epiphysis (Nos. M.54115 & M.54116)
The two pieces represented include a larger morph (M.54116) and a smaller one (M.54115), which are otherwise very similar in their preserved portions (Figs 1–4). They are notable primarily for their implied relatively high neck-shaft angles. On both of them, estimating the proximal diaphyseal and neck axes provides neck-shaft angles in the vicinity of 130° and probably greater than 130°. In this, they are within the range of European late Upper Paleolithic human remains [$125.0^{\circ} \pm 5.8^{\circ}$, N = 7 (Trinkaus, 1993)] but towards the upper end of that range.

Proximal Diaphysis (Nos. M.54117 to M.54122)
There are five pieces of proximal lateral femoral diaphysis which preserve portions of the gluteal tuberosity and adjacent proximal lateral diaphyseal (or gluteal) buttress, four left and one right and all representing the smaller morph (Figs 5, 6).

All of these pieces are notable for their prominent, rugose, and medio-laterally concave gluteal tuberosities. The available dimensions of these tuberosities are in Table 1, even as minimum dimensions

Table 1 Gluteal tuberosity dimensions of proximal femora.

	Tuberosity breadth (max.), mm	Tuberosity depth (max.), mm
M.54117	9.0	2.1
M.54118	≥9.5	1.5
M.54119	>8.0	≥2.1
M.54120	≥8.3	≥1.6
M.54121	≥10.2	≥1.8

Table 2 Cortical thicknesses (in mm) of proximal lateral femoral diaphyses.

	Gluteal buttress maximum	Anterior diaphysis	Antero-lateral diaphysis	Posterior diaphysis
M.54117	10.4	3.8	–	4.8
M.54118	11.3	–	4.5	6.7
M.54119	10.7	–	ca.4.0	3.4
M.54120	ca.11.1	–	4.8	5.1
M.54121	10.3	4.2	–	5.0

for most of the pieces, they are well within the ranges of variation of late Upper Paleolithic humans [7.8 ± 2.0 , N = 5 (Trinkaus, 1976)]. The dimensions of these tuberosities become more pronounced when they are placed in the context (albeit qualitatively) of the small dimensions of these diaphyses.

These pieces are also notable for their pronounced proximo-lateral buttresses (Figs 5, 6). The relative dimensions of these buttresses can be assessed in part by comparisons of maximum cortical thickness across the buttress compared to those obtained from adjacent anterior, antero-lateral and posterior diaphyseal bone (Table 2). In all but one case the buttress thickness is more than twice the largest adjacent cortical thickness, and in the exception it is still 69% larger than the posterior diaphyseal thickness.

There is one piece which preserves the medial diaphysis with the spiral line. It has a modest but clear spiral line and exhibits some thickening of the medial cortex. The maximum medial cortical thickness of 8.0mm is slightly larger than those of the adjacent anterior (5.7mm) and posterior (7.5mm) cortical bone. It represents one of the larger morphs.

Mid Diaphysis (Nos. M.54081, M.54123 & M.54124)
This region is represented by two diaphyseal pieces of the larger morph (M.54081 and M.54124) and two that are indeterminate as to relative size. One of them preserves the more proximal portion of the posterior midshaft (M.54124) whereas the other two appear to be generally closer to midshaft.

Each of the three specimens (Figs 7, 9, 10) presents a relatively rugose linea aspera, with an adjacent concave lateral subperiosteal diaphyseal surface and the formation of a pilaster. On the specimen with the strongest development of the linea aspera, M.54081, the linea aspera is 8.6mm wide at the level of the nutrient foramen and 11.1mm wide more distally, where it is broken postmortem (Fig. 10). The two specimens with the linea aspera preserved near midshaft present posterior cortical thicknesses (across the linea aspera) of 9.7mm (M.54081) and 9.3mm (M.54123, Fig. 7), which can be compared to a lateral thickness of 5.0mm on the former and a medial one of 5.5mm on the latter.

Distal Diaphysis (Nos. M.54085, M.54125)
The two specimens of distal posterior femoral diaphysis present little of note morphologically, and one of them (M.54085) is sufficiently amorphous that its identification as a distal posterior femoral shaft can be questioned.

The more complete specimen (M.54125) is from a late juvenile or early adolescent (Fig. 11), with clear formation of the metaphyseal surface but an uncertain degree (given preservation) of interdigitation between the metaphysis and the epiphysis. The only feature of note is the presence of porous periosteal new bone on the posterior surface above the medial condyle metaphyseal surface, covering an area extending proximally 32.1mm from the epiphyseal line and at least 18.7mm wide (its medial boundary extends beyond the medial postmortem break). Given the isolated nature of this specimen, it remains unclear whether the periosteal reaction is the result of a localized infection or part of a systemic disorder.

TIBIAE

Inventory

M.54088 (GC 87 60B)

Right

Posterior half of an immature (unfused) medial condyle. Maximum depth: 19.2mm, maximum breadth: 27.2mm.

M.54089 (GC 87 122A)

Left

Postero-lateral section of an immature medial condyle. Maximum depth: 25.7mm, maximum breadth: 22.4mm.

M.54091 (GC 87 119E)

Left

Diaphyseal section with the interosseus line from just distal of the tibial tuberosity to near midshaft (Fig. 16). Maximum length: 117.8mm, maximum breadth: 18.8mm.

M.54092 (GC 87 76)

Left

Midshaft anterior crest, medial surface and a small amount of the lateral surface (Fig. 15). Maximum length: 173.8mm, maximum breadth: 28.5mm.

M.54093 (GC 87 119B)

Right

Portion of the posterior diaphysis with the soleal line and the nutrient foramen. Maximum length: 67.5mm, maximum breadth: 27.9mm.

M.54126 (GC 50-51)

Side indeterminate

Midshaft section with the anterior crest and the medial side (Fig. 12). Maximum length: 99.2mm, maximum breadth: 31.9mm.

M.54127 (GC 87 43)

Side indeterminate

Anterior crest of a midshaft section, with little of the medial or lateral surfaces (Fig. 14). Maximum length: 105.9mm.

M.54128 (GC 87 60D)

Side indeterminate

Mid posterior proximal epiphyseal bone, with the irregular surface bone from just below the capsular line. Maximum length: 39.3mm, maximum breadth: 27.6mm.

M.54129 (GC – no number)

Side indeterminate

Heavily encrusted anterior midshaft section, which is possibly non-human (Fig. 13).

Morphology

Proximal Epiphysis (Nos. M.54088 & M.54089)

The two pieces of immature (unfused) medial epicondyle epiphysis

Table 3 Anterior and medial cortical thicknesses of midshaft tibial diaphyseal fragments. The proximo-distal location of midshaft is approximate given fragmentation. Measurements in millimeters.

	Anterior cortical thickness	Medial cortical thickness
M.54092	12.9	3.2
M.54126	14.6	5.8
M.54127	10.3	–
M.54129	6.9	3.3

present gentle medio-lateral concavities of the articular surface, small and blunt intercondylar eminences, and clear *M. semimembranosus* sulci posteriorly.

Anterior Diaphyseal Sections (Nos. M.54092, M.54126, M.54127, M.54129).

The four preserved sections of anterior, approximately midshaft, crest represent two large individuals (M.54092 & M.54126) and two smaller ones (Figs 12–15). They exhibit considerable variability in anterior cortical thickness (Table 3), with the ratio between the maximum anterior and medial thicknesses varying from 2.1 to 2.5 to 4.0. One of the specimens, M.54127, has a relatively sharp anterior margin, whereas the others exhibit clear but blunt anterior crests.

Posterior and Lateral Diaphyseal Sections (Nos. M.54091, M.54093 & M.54128)

These three pieces include an otherwise amorphous piece of proximal dorsal diaphyseal surface, a piece of the lateral proximal diaphysis with a very clear and slightly raised interosseus line (Fig. 16), and a proximal dorsal piece with a modest soleal line associated with a clear flexor line between the *M. tibialis posterior* and *M. flexor digitorum longus* proximal origins.

FIBULA

Inventory

M.54094 (GC 87 42/54/55)

Left

Diaphyseal section, mostly preserving the soleal and peroneal surfaces (Fig. 17). Maximum length: 162.7mm, maximum breadth: 12.4mm.

Morphology

The fibular diaphyseal piece (Fig. 17) preserves areas for the *M. soleus* and *M. peroneus longus*, but the preserved dorsal surface is smooth and presents no clear muscle markings. Otherwise, the diaphysis appears relatively straight, but it not sufficiently intact to indicate whether there is mid or distal shaft lateral convexity.

Fig. 10 Posterior view right femoral midshaft, M.54081.

Fig. 11 Posterior view of left immature distal femoral metaphysis, M.54125.

Figs 12–15 Anterior views of tibial anterior diaphyseal pieces; **12**, M.54126; **13**, M.54129; **14**, M.54127; **15**, M.54092.

Fig. 16 Lateral view of a mid/proximal lateral diaphyseal piece of a left tibia, M.54091.

Fig. 17 Posterior view of left fibular diaphysis, M.54094.

Fig. 18 Dorsal view of left anterior calcaneus, M.54095.

Fig. 19 Medial view of medial cuneiform bone, M.54096.

Figs 20–22 Lateral views of left metatarsals 3 to 5; **20**, M.54144; **21**, M.54097; **22**, M.54098.

All figures $\times 0.95$.

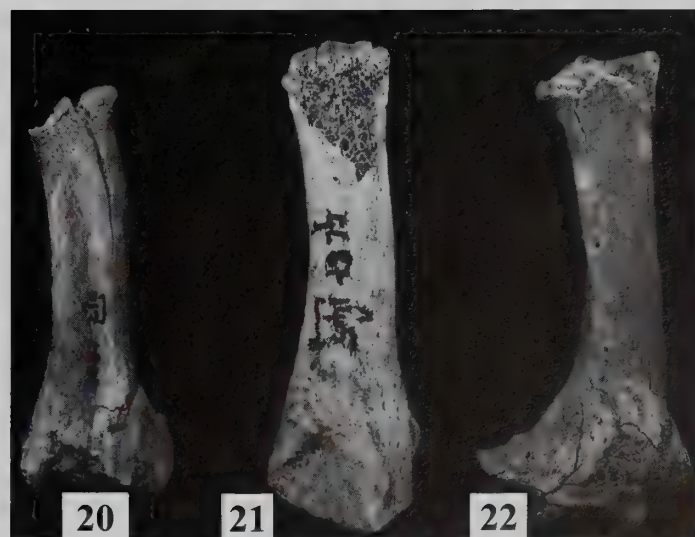
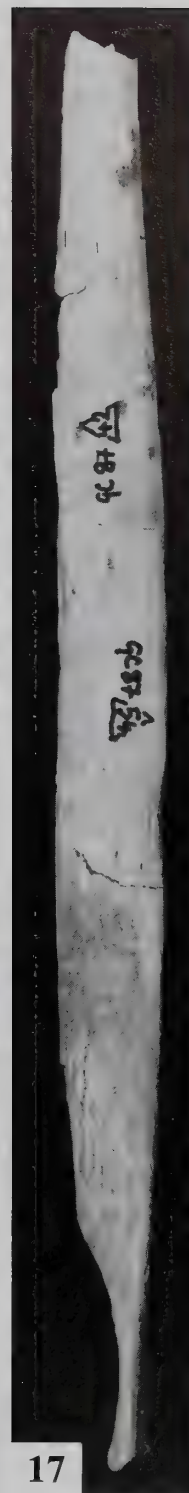
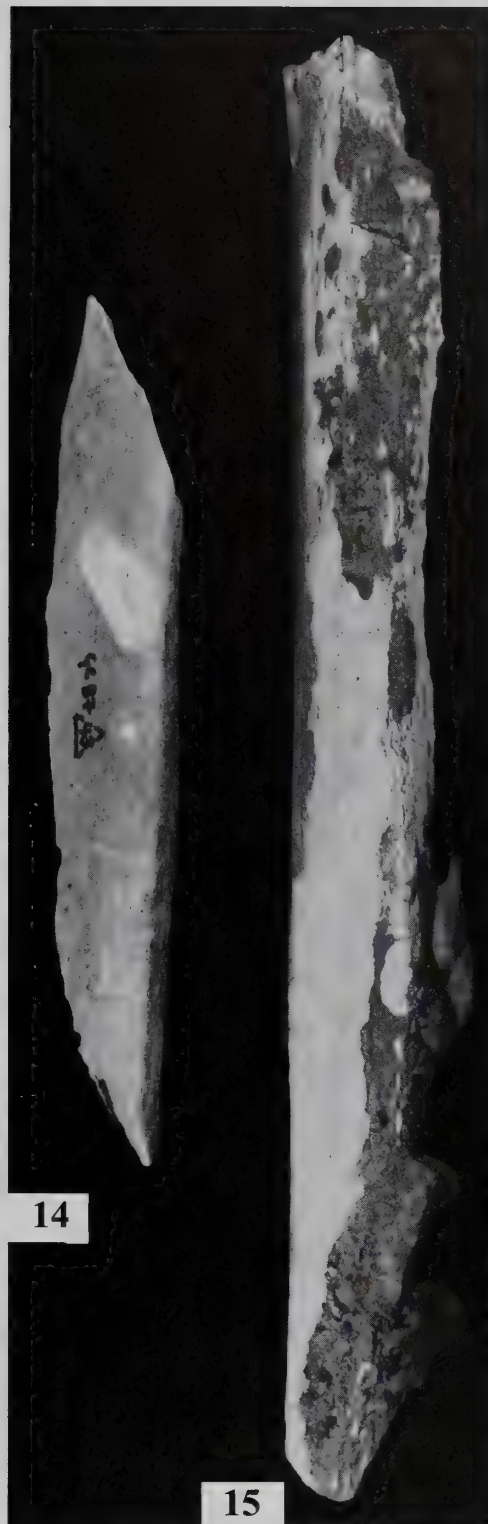
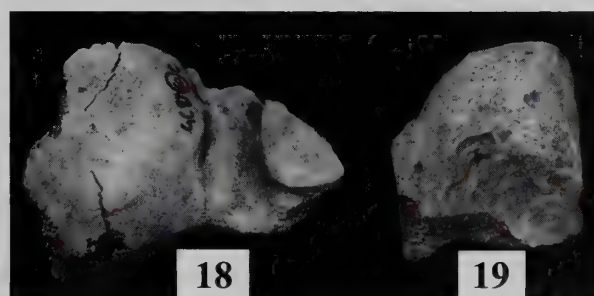
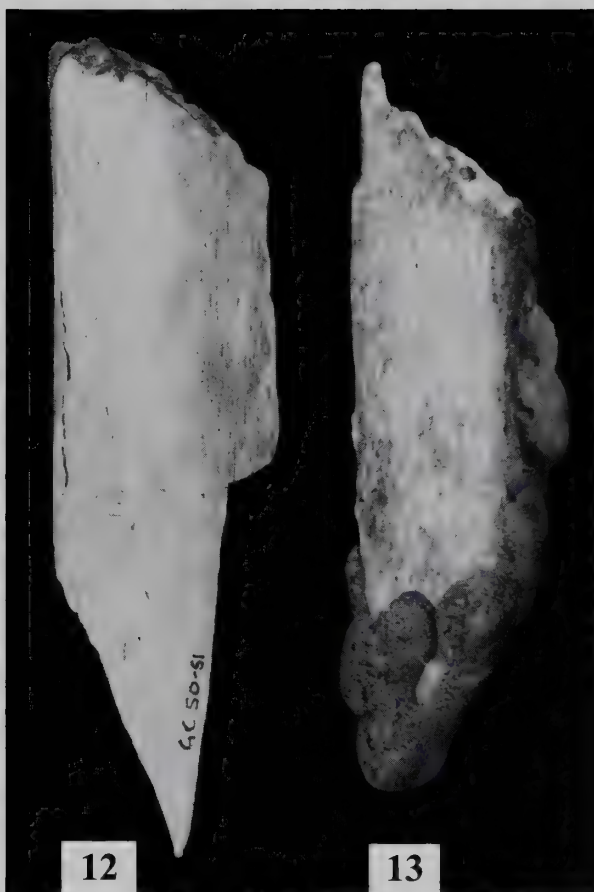
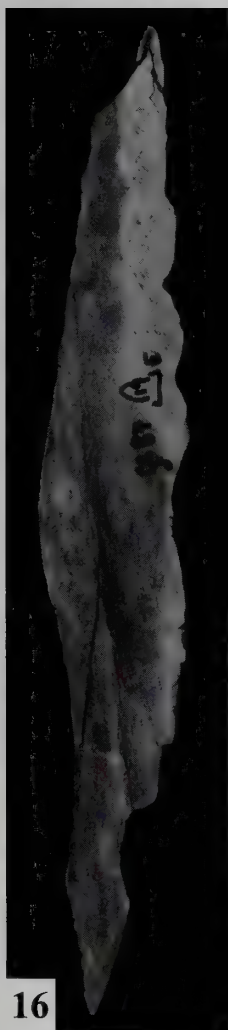
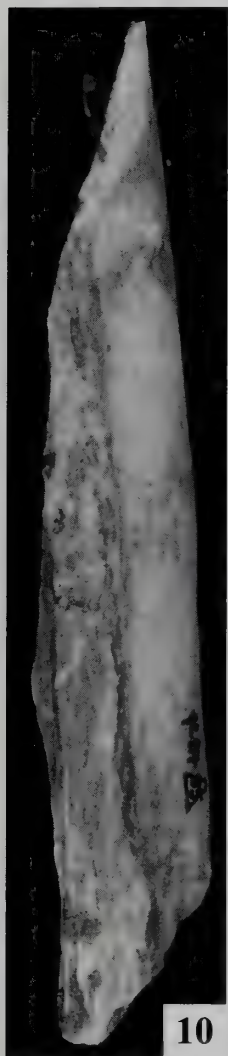


Table 4 Osteometrics and midshaft cross-sectional geometry of the metatarsal proximal epiphyses and diaphyses. Cross-sectional geometric properties are computed from radiographically determined external diameters and cortical thicknesses (corrected for parallax) using ellipse formulae (see Runestad *et al.*, 1993). All measurements in millimeters.

	MT3 –M.54144	MT4 –M.54907	MT5 –M.54098
Midshaft height	9.9	10.0	8.0
Midshaft breadth	6.2	9.0	9.9
Shaft curvature chord ^a			31.1
Shaft curvature subtense ^a			0.8
Total area (mm ²)	48.2	70.7	62.2
Cortical area	37.9	48.0	44.3
Medullary area	10.3	22.6	17.9
Antero-posterior 2nd moment of area (I_x) (mm ⁴)	278.9	398.3	224.6
Medio-lateral 2nd moment of area (I_y) (mm ⁴)	111.5	319.6	354.2
Polar moment of area (mm ⁴)	390.3	717.9	578.8
Proximal articular height ^b	–	16.9	–
Proximal articular breadth ^b	–	9.7	–
MT4 facet height ^c	–		11.1
MT5 facet height ^c		12.3	
MT5 facet length ^c		10.0	

^a Chord and subtense along the medial (or dorso-medial) diaphysis between the epiphyseal swellings, with a positive subtense indicating medial convexity.

^b Dorso-plantar height and medio-lateral breadth of the tarsal articulation.

^c Dorso-plantar height and proximo-distal length of the intermetatarsal facets.

CALCANEUS

Inventory

M.54095 (GC 87 60C)

Left

Fragment preserving the medial and posterior portion of the posterior talar surface and the posterior portion of the sustentaculum tali and medial articular surface (Fig. 18). Maximum AP: 29.7mm, maximum breadth: 33.3mm.

Morphology

There is little of morphological note on this piece (Fig. 18), other than that the margins for the posterior and medial talar facets along the sulcus tali appear sharp and distinct, and there is no porosity between them. Although standard osteometrics are not possible, this bone appears to derive from a large individual.

MEDIAL CUNEIFORM

Inventory

M.54096 (GC 87 199)

Left

Largely intact bone, with damage to the plantar surface (Fig. 19). Maximum antero-posterior length: 22.2mm, maximum dorso-plantar height: 23.1mm.

Morphology

The one surface of note on this specimen (Fig. 19) is its metatarsal 1 facet, which is smooth, medio-laterally flat, and shows no sign of being divided into dorsal and plantar portions. Its superior length is 20.0mm and its middle length is 20.6mm.

METATARSALS

Inventory

M.54144 (GC 87 30)

Left

Metatarsal 3 diaphysis with the proximal epiphysis largely lost to damage and the distal epiphysis unfused and lost (Fig. 20). Maximum length: 51.7mm.

M.54097 (GC 87 145)

Left

Metatarsal 4 diaphysis and damaged proximal epiphysis, missing the unfused distal epiphysis (Fig. 21). Maximum length: 57.8mm.

M.54098 (GC 87 210)

Left

Metatarsal 5 diaphysis lacking the unfused distal epiphysis and most of the proximal epiphysis to damage (Fig. 22). Maximum length: 47.1mm.

Morphology

The three preserved metatarsal specimens derive from the same foot (Table 4; Figs 20–22). They show little muscular marking, possibly due to their immature status. The metatarsal 4 and 5 diaphyses are relatively round, and the metatarsal 5 diaphysis presents little medial diaphyseal convexity.

DUBIOUS FRAGMENTS

The following diaphyseal fragments have been included with the human material. They are either clearly non-human or so fragmentary as to be insufficient to determine whether they are human. They do not provide morphological information even if they are in fact hominid, and are therefore not included in the above descriptions, but are listed here for future reference.

<i>Cat. no.</i>	<i>Excavation no.</i>
M.54082	GC 87 154
M.54083	GC 87 221A
M.54084	GC 87 110
M.54086	GC 16 1950-51
M.54099	GC 87 5
M.54100	GC 87 40
M.54101	GC 87 153B
M.54102	GC 87 118C, GC 87 118D
M.54103	GC 87 122I, GC 87 122J
M.54104	GC 87 123A
M.54105	GC 86 23
M.54106	GC 87 226C
M.54107	GC 87 173A
M.54108	GC 87 173-B
M.54109	GC 87 173-C
M.54110	GC #1021.0
M.54111	GC 86 6 #1002.0
M.54112	GC 89 001
M.54113	GC 89 016
M.54114	GC 87 165B

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